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[*Authors alone are responsible for all opinions expressed in their Communications.*]

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THE

SCIENTIFIC PROCEEDINGS

OF

THE ROYAL DUBLIN SOCIETY

No. 1.

IRISH PREVIOUSLY SPAWNED SALMON

By

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In recent times there has been considerable discussion, in angling and sporting journals, on the subject of previously spawned salmon. To date no information has been available for any one country as to the proportion of previously spawned fish in the different rivers in any one year, or how these proportions may vary from year to year. In Ireland there are varied views on the value of the "returned kelt" in the stocks of salmon of a river. Some people hold that they are valueless, and others that the larger members of the salmon stocks are previously spawned fish.

The idea that very large salmon must have spawned on at least one occasion is one which "dies hard", despite many investigations in which it has been shown to the contrary. Of course, if one considers the stocks of salmon in a river where the majority of fish are very small, *i.e.*, a large proportion are grilse or peal, then it is true that the heavier members of the stocks will contain a larger proportion of previously spawned fish than the lighter ones. This is shown clearly in the case of the Ballisodare River (Went, 1941, p. 343, Table 9), and, no doubt, applies equally well to other similar rivers. In rivers where the average weight is high the larger members of the stocks are invariably maiden or unspawned fish. For example, during the 1944 season the present author examined the scales of a fair number of large salmon, weight 35 lb. or over, from various rivers throughout Éire. Not a single specimen of a previously spawned fish was noted. In all our investigations into Irish salmon, only two previously spawned fish weighing over 35 lb. have been encountered. The first (37·5 lb.) was recorded by Southern (1928, p. 58) from the Shannon, and the second (37·0 lb.) by the present author from the Corrib (1943, p. 284). Taking the recorded data from the Shannon alone, 24 very large spring

fish have been examined having a total weight of 1,011·4 lb. or an average weight of 42·2 lb. Weights up to 56 lb. 10 oz. have been recorded from the Shannon in these investigations.

In the autumn of 1943 the Fisheries Branch of the Department of Agriculture was approached by persons interested in the River Lee for information on the subject of previously spawned fish in that river. No investigations have been carried

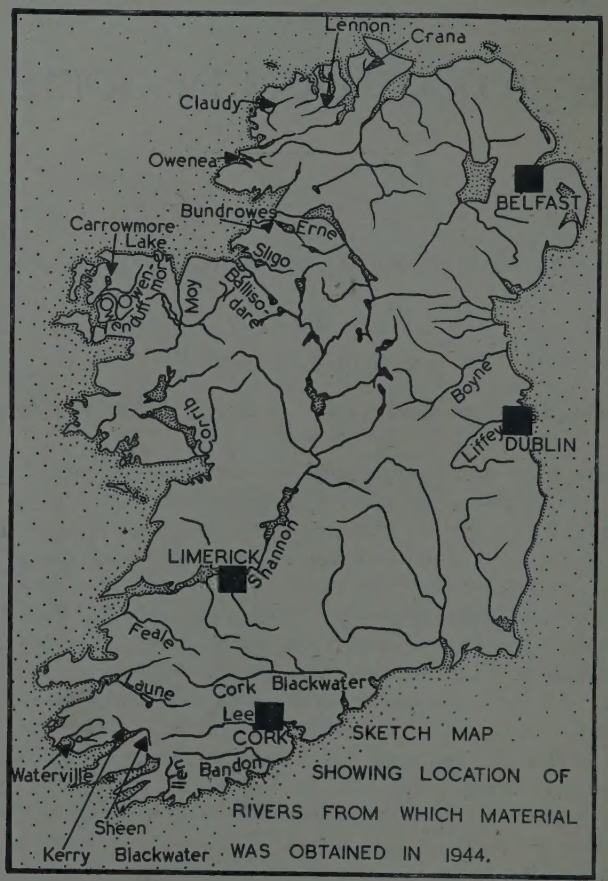

Fig. 1.

out on the River Lee, and it was naturally impossible to give any information on the subject. It was, however, suggested to the persons interested in the matter that if they were willing to collect the necessary material the officers of the Department would work it out. Owing to the stress of other work it was not found possible, at that time, to carry out a full scale investigation into the salmon of the River Lee, but in view of the widespread interest in the subject of previously spawned fish it was decided to extend a modified form of investigation so as to include a number of other rivers in the country. (see map).

Table 1. Showing sources of material and collectors. The rivers are arranged clockwise from Dublin.

River	Name and Address of Collector	River	Name and Address of Collector
Liffey	The late Captain F.H. ffrench Davis, Salmon Pool House, Dublin	Moy	Mr. W.P. Stevens, Moy Fisheries, Ballina, Co. Mayo.
Blackwater (Cork)	Mr. G. FitzGerald, Lismore Estates Co., Lismore, Co. Waterford.	Ballisodare	Mr. F.P. Scott, The Rapids, Ballisodare, Co. Sligo.
Lee	Mr. J. Scanlon, 53 South Mall, Cork	Sligo	Mr. W.T. Middleton, Collooney, Co. Sligo Mr. J. Jenkins, Sligo.
Bandon	Mr. W.J. Seymour, Dunderrow, Kinsale, Co. Cork.		
Ilen	Mr. J. Beamish, Skibbereen, Co. Cork.	Bundrowes	Mr. J. Cassidy, Bundrowes, Bundoran, Co. Donegal.
Sheen	Mr. W. Johnstone, Estate Office, Kenmare, Co. Kerry.	Erne	Mr. T. MacD. Swan, Erne Fisheries, Ballyshannon, Co. Donegal.
Blackwater (Kerry)	Colonel E. Hood, Dromore Castle, Kenmare, Co. Kerry.	Owenea	Mr. F.A. Watson, Riversdale House, Glenties, Co. Donegal.
Waterville	Mrs. H. Butler, Waterville House, Waterville, Co.Kerry	Claudy	Mr. W. Hunt, The Hotel, Gweedore, Co. Donegal.
Laune	Mr. A. de C. Dodd, K.R.D. Fisheries, Killorglin, Co. Kerry.	Lennon	Sir Harry Stewart, Bart., Fort Stewart, Co. Donegal.
Feale	Mr. G. Gleasure, The Square, Listowel, Co. Kerry.	Crana	Mr. I.J. Trew Colquohoun, Buncrana, Co. Donegal.
Shannon	Mr. L. Forde, Shannon Fisheries, Limerick.	Boyne	Mr. P.J. Tiernan, Oldbridge, Co. Meath. Captain R. Law, Rosnaree, Slane, Co. Meath.
Corrib	Lt. Colonel E.G.K. Cross, D.S.O., Weir House, Galway.		
Owenduff (Ballycroy) Owenmore Carrowmore Lake	Mr. P.J. Lenehan, Croy Lodge, Ballycroy, Co. Mayo.		

Table 2. Percentage of previously spawned fish.

Month	River												
	Liffey	Blackwater (Cork)	Lee	Bandon	Ilen	Sheen	Blackwater (Kerry)	Waterville	Laune	Feale	Shannon	Corrib	Owenduff
Jan.	-	-	-	-	-	-	-	5.5	2.9	-		-	-
Feb.	0.8	-	0.2	-	-	-	-	7.0		-	6.9	23.5	-
March	0.8	2.9	1.7	-	-	-	-	Nil	2.8	-		10.7	-
April		1.6	1.0	-	-	-	Nil		0.8	1.1	3.9	12.0	1.9
May		1.4	2.1	-	1.8	-	6.0	6.1	2.5	1.2	1.2	2.2	Nil
June	Nil	0.9	3.0	-	7.2	-	5.2		4.2	2.2	2.1	5.9	3.8
July		5.0	Nil	-	12.4	-	5.4		5.4	6.8	10.5	19.0	11.6
Aug.		-	Nil	-	-	-	-	-	-	-	-	-	-
Total	0.6	2.5	1.2	8.3	8.2	3.3	5.1	5.8	3.3	1.8	4.1	7.5	4.1

Month	River												Total for all rivers examined
	Owenmore	Carrowmore Lake	Moy	Ballisodare	Sligo	Bundrowes	Erne	Owenea	Claudy	Lennon	Crana	Boyne	
Jan.	-	-	-	-	5.7	-	-	-	-	-	-		5.5
Feb.	-	Nil	17.3	-	Nil	6.9	-	-	-	-	-	Nil	2.6
March	-	0.6	4.8	-	5.0	6.8	11.6	-	-	-	-	0.7	3.3
April	-	Nil	5.0	8.2	Nil	7.2		-	-	-	-	1.3	3.8
May	-	5.5	1.9	8.9	Nil	5.2		-	-	-	Nil	1.0	2.3
June	-	4.6	3.2	1.9	3.3	4.0	8.8	-	-	-	5.7	0.8	4.4
July	-	-	6.0	0.8		16.9		-	-	-	-	2.2	6.7
Aug.	-	-	-	-	-	-	-	-	-	-	-	2.5	2.7
Total	10.2	1.4	4.3	2.4	4.5	7.3	9.5	2.0	1.3	7.4	5.4	1.2	4.3

Table 3. Comparison of present results with those from previous investigations.

River	Reference to previous publication	Proportion of previously spawned fish	
		1944	Previous result
Ballisodare	Went, 1941, p. 342	2.4%	4.8% and 4.7%
Owenduff	Went, 1941, p. 178	4.1%	4.9%
Erne	Went, 1942, p. 475	9.5%	6.4%
Corrib	Went, 1943, p. 295	7.5%	6.0%
Waterville	Went & Barker, 1943, p. 100	5.8%	7.2%
Shannon	Went, 1943, p. 172	4.1%	5.6%
Liffey	Unpublished data	0.6%	2.3%

The material consisted of a single scale, taken from just below the dorsal fin, from as many fish as possible. The scales from the different months were preserved in separate bottles in ordinary water. If the water was changed regularly the scales became free from slime and remained in a satisfactory condition for examination, although, if the water was not changed often, the scales underwent rapid deterioration. In all 28 persons were approached, and of these 25 undertook to collect and, what is more important, did collect material relating to the rivers in which they were interested. In Table 1 a list of rivers investigated has been given together with the names of persons collecting the material. The author wishes to take this opportunity of thanking the collectors for their collaboration in this investigation.

Not all the scales collected in the manner described above are suitable for age determination, as some are replacement scales (*i.e.*, scales which have replaced an original scale lost during some period of life). There is no reason, however, to believe that the elimination of such scales and the investigation of the remaining suitable scales would introduce any error in the results.

In all 25,029 scales were examined, of which 1,078 or 4·3% were from previously spawned fish. Only 12 out of the 1,078 fish bearing spawning marks on their scales, or 1·1% of the previously spawned fish, had spawned previously on two occasions. Not a single specimen of a fish which had spawned three or more times previously was encountered. The proportions of previous spawners in the different rivers have been given in Table 2, only the percentage of the total run being indicated where the number of scales examined did not exceed 300. In the case of the 19 rivers shown below more than the minimum amount of material (300 scales) was available. They have been arranged in order of the percentage of previous spawners.

(1) Liffey *P*	....	0·6%
(2) Boyne *P*	....	1·2%
(3) Lee *P*	....	1·2%
(4) Carrowmore Lake *L*	....	1·8%
(5) Feale *P*	....	1·8%
(6) Ballisodare *L*	....	2·4%
(7) Cork Blackwater *P*	....	2·5%
(8) Laune *P L*	....	3·3%
(9) Shannon *P L*	....	4·1%
(10) Owenduff *P*	....	4·1%
(11) Moy *L*	....	4·3%
(12) Sligo *L*	....	4·5%
(13) Kerry Blackwater *L*	....	5·1%
(14) Crana	....	5·4%
(15) Waterville *L*	....	5·8%
(16) Bundrowes *L*	....	7·3%
(17) Corrib *L*	....	7·5%
(18) Ilen *P*	....	8·2%
(19) Erne *P L*	....	9·5%

The Letter *P* adjacent to the name of a river indicates that there is an important public or private fishery in tidal waters which is intensively fished, while the letter *L* indicates that there are one or more lakes on the river system.

From the foregoing table it would appear that where there is a large commercial fishery on the tidal waters, there is a tendency for the proportion of previous spawners to be low. On the other hand, where there are one or more lakes on the river the proportion of previous spawners would appear to be high. There are two notable exceptions to this in the Ballisodare River and the River Ilen. The Ballisodare River has on the course of one of its tributaries a fairly large lake (Lough Arrow), but, as will be seen from the map of the watershed of the river given in Went, 1940 (p. 291), salmon do not enter the lake, which may provide an explanation of this apparent discrepancy. In the case of the Ilen no such explanation can be given, but it might be pointed out that the river is a very short one. The Erne is a river which has a large public fishery in its tidal portion, but there is also a lake on the river, the majority of salmon having to pass through this lake before spawning.

It might now be asked how the present results compare with those from previous full scale investigations on Irish rivers. In Table 3 the comparison has been given. With the exception of the Rivers Corrib and Erne the proportion of previously spawned fish was less in 1944 than in the years investigated previously.

As we have a fairly large number of rivers represented in each month of the season we might assume, without being over-speculative, that the monthly combined figures apply in some degree to the country as a whole. In Table 4 the material from each month has been pooled and the proportion of previous spawners calculated.

TABLE 4.

Month	Number of scales examined			Percentage of previous spawners
	With SMs.	Maiden	Total	
January	40	693	733	5·5%
February	38	1,398	1,436	2·6%
March	81	2,370	2,451	3·3%
April	101	2,580	2,681	3·8%
May	77	3,223	3,300	2·3%
June	402	8,835	9,237	4·4%
July	334	4,673	5,007	6·7%
August	5	179	184	2·7%
TOTAL	1,078	23,951	25,029	4·3%

The estimated proportion of previous spawners for the country as a whole is therefore 4·3%, or, put into another form, the previously spawned fish are equivalent in number to approximately two-thirds of the total catch in Éire by

single rod and line. From this it would appear that the " returned kelts " in most rivers contribute a fairly substantial quota to the stocks of salmon.

That only about one in every twenty fish entering a river is a previous spawner has led to the belief in the great destruction of kelts after spawning. It is unnecessary to cite the many statements throughout the angling literature that 95% or more of fish which have spawned, fail to return to the river for a second time. This misconception can be explained simply in the following way. If we assume that *every salmon survived one spawning*, then with regular runs of salmon of the same strength the proportion of previous spawners would be 50%. In other words a *survival rate of* 100% would, with runs of constant strength, only produce 50% previous spawners. Mr. J. A. Hutton in a recent contribution to the *Fishing Gazette* (No. 3,496, Vol. 126, 22nd April, 1944, pp. 196–197) shows that in the case of the Wye the survival of female kelts was about 20% and those of the males 1·2%, the results for both sexes combined being 10·8%. There is no doubt that male kelts do not survive to make a second return to fresh water as clean fish to the same extent as the females, as the proportion of male previous spawners is usually much less than that of the female previous spawners. Naturally the information for Éire is not as complete as that for the Wye, but in at least two rivers the information available is interesting.

The Waterville (Currane) River is peculiarly circumstanced in that, owing to its narrowness, the fishing weir is carried completely across the river by the authority of an order made by virtue of Section 11 of 26 and 27 Vic. Cap. 114. Instead of the normal two-day weekly close period, however, in this river the weir is open for the free passage of fish for a period of 72 hours. (See Went and Barker, 1943). During the weekly fishing period, therefore, virtually all the salmon entering the river are taken by either the weir or the net operated downstream therefrom. Let it be assumed that 1,000 fish enter Ballinskelligs Bay for the purpose of running ultimately into the Waterville River. Of these fish a quantity, estimated at about 150 in number, will be taken by the open Bay seine nets, leaving 850 to enter the river proper. Of these, four-sevenths on an average will be taken by the weir and net, leaving three-sevenths, or 365 fish, to ascend the river. The *Statistics of Salmon, Sea Trout and Eels* published by the Fisheries Branch of the Department of Agriculture, indicate that from 1927 to 1939 the rod catch was 15·8% of the catch by commercial methods in the Waterville Fishery District in which the Waterville or Currane River is the principal salmon river. Even assuming that only 10% of the net and weir catch, say 64 fish, is taken by the rods then the escapement for spawning will not exceed 301 fish. Assuming that the results obtained in this investigation for the Waterville River apply generally from year to year, each 1,000 fish originally coming in from the sea would contain 58 previous spawners. In other words an escapement of 300 fish, which were allowed to spawn, provides 58 previous spawners in future years or a survival of the spawned fish at a rate of 19·3% for both sexes.

Now let us pass to the Shannon, where accurate records of the fish entering the freshwater portion of the river are available. Shannon salmon are subjected to capture on the estuary of the river by three types of engines, namely (1) Stake Weirs, (2) Drift nets, and (3) Draft nets. After careful consideration of all the

factors involved the author considers that about 25% of the run of salmon native to the Shannon proper above Limerick are taken before reaching Thomond Weir operated by the Electricity Supply Board (Shannon Fisheries). Thus out of every 1,000 fish originally available 750 fish escape the various fishing engines in the Lower Shannon to enter Thomond Weir. This weir is operated without a free gap or passage for fish, by special authority of an Order of the Minister for Agriculture, by virtue of the provisions of the Shannon Fisheries Act of 1938, for what is virtually the whole of the runs of salmon throughout the season (see Went, 1943). The proportion of salmon which the Shannon Fisheries are now authorised to take is 28% of the total run, or 210 fish from our original 1,000 fish, leaving 540 fish to pass upstream. In the Shannon proper the proportion of rod-caught fish to those taken by commercial methods would probably not exceed 10%, but, allowing a total of 20% for all exigencies, about 440 fish would be left to propagate the species. From Table 2, however, it is clear that 41 out of every 1,000 fish entering the river are previous spawners, having been derived from 440 spawning fish, giving a survival rate for both sexes of 9·4%, which agrees quite closely with the Wye figures mentioned previously.

Fishing for kelts was practised on the River Lee over a century ago, but even in those days it was recognised that the food value of these fish was slight. Fortunately, since that time enlightened opinion has changed with respect to the taking of kelts for food. As Mr. Hutton records, nature at no cost to ourselves transforms small quantities of almost inedible fish into quantities of " most excellent and nourishing diet " *Fishing Gazette* (No. 3,496, Vol. 126, p. 197). He gives an example of a kelt weighing 8 lb. transformed in 15 months to a clean 28 lb. fish. In Ireland over a period of years a large number of stripped fish (kelts) have been marked at the various hatcheries. The results given by Hillas, 1905, and those obtained since 1915 have been combined in Table 5.

TABLE 5

	River								Total all Rivers
	Bann	Foyle	Owenea	Erne	Aasleagh	Laune	Blackwater (Cork)	Slaney	
Number of fish examined	15	14	96	5	1	5	2	1	139
Total Weight of Kelts in lb.	75	66½	531	26	11½	26	16¼	11	763¼
Total Weight of clean fish in lb.	170	136	1,022	54¼	18	61½	30	27	1,418¾
Increase in weight (percentage)	127	105	93	108	57	136	85	145	98

The total shows that the kelts after recovery weighed almost double their original weight, apart from any question of the quality of the resultant material. Surely this alone furnishes a good reason for the protection of the kelt.

That the proportion of females which survive spawning is greater than that of the males is well known, but the fact that some male kelts do survive to return for a second time as clean fish is obvious from the marking of kelts which has been carried on in many places. In the Owenea in County Donegal 2,875 kelts have been marked in the past twelve years. Of these 1,969 were females and 906 males. The recaptures of clean marked fish totalled 127, of which 106 were females and 21 males. The survival rate of the females compared with the males from these results is 2·35 to 1.

Mr. Hutton, in the article in the *Fishing Gazette* already referred to in another connection, stated by way of conclusion " Therefore I have no hesitation in saying that kelts are well worth preserving, and that it would be a most stupid mistake to make it legal to kill them, for even the best ' mended ' kelt is most unpalatable food and provides very little real nourishment." The results of the present preliminary investigation confirm Mr. Hutton's views, and show clearly *why it is illegal to kill salmon kelts*. It is hoped to repeat the investigations in future years so that we might have, in relation to Irish salmon, some idea of the proportions and fluctuations in the numbers of previously spawned fish. In this matter, however, the co-operation of the owners of the various fisheries is essential. Fortunately most of the owners of important commercial fisheries in Ireland have been ready to give us every assistance in these investigations, and it is not anticipated that there will be any change in this respect in future years.

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No. 2.

OBSERVATIONS ON *GIBBERELLA SAUBINETII* (MONT.) SACC. ON CEREALS IN IRELAND IN 1943 AND 1944.

By

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(Plate 1.)

[Read February 27. Published separately May 22, 1945].

Following the severe outbreak of *Gibberella Saubinetii* on wheat in this country in 1942 (4), observations on the occurrence and prevalence of this fungus on cereals were continued in 1943 and 1944. Some investigations were also carried out at the Albert Agricultural College, Glasnevin, on the development of "Seedling Blight" and on the general infection of the host. The results are presented in the accompanying paper.

Natural Occurrence of "Seedling Blight" of Wheat in 1943.

Failures of wheat brairds were reported as being rather common in the spring of 1943, the worst misses occurring in crops sown in February, March, and April. A number of samples of the seed sown and small seedlings from infected fields in several counties were examined. In all cases investigated the specimens came from fields in which the brairds were exceptionally poor. Many of the ungerminated grains which were collected in these fields were reddish or carmine in colour, and were found to be permeated throughout with the fungus *Gibberella Saubinetii*. The specimens of plants received at the same time were small, chlorotic, and their root system poorly developed. Many of those roots present were brown and rotting, and some of the seedlings were dead and others dying. Incubation of these plants under moist warm conditions, in the majority of cases, gave conidial fructifications of *G. Saubinetii*. There is no doubt that the poor brairds in these cases of spring-sown wheat were mainly due to using badly infected seed. Furthermore the investigations established the facts that "Seedling Blight" of wheat occurred in

the following counties, Limerick, Clare, Westmeath, Offaly, and Dublin, and that this phase of disease caused by *G. Saubinetii* is one which must be reckoned with, especially in seasons following wet years when scabbed wheat has been prevalent. Moreover, plants which have been killed off by "Seedling Blight," later in the growing season are a potential source of infection for "Ear Blight," as will be shown further on.

The Occurrence and Prevalence of "Ear Blight" and "Scab" on Cereals in 1943.

The term "Ear Blight" is that applied to infected cereal heads where only the *Fusarium* stage of the fungus is present, whereas when "Scab" is used it implies the presence of perithecia containing ascospores of *Gibberella Saubinetii*.

As a result of instructions issued by the Department of Agriculture to the various Instructors and Overseers in Agriculture, 82 samples of wheat (in ear) and 1 sample of threshed grain were submitted for examination in 1943, as being suspected of "Ear Blight" or Cereal "Scab". Of these, 62 samples showed the presence of *G. Saubinetii*, 26 of them showing only the conidial stage of the fungus, and 36 having well-developed perithecia containing ascospores. This "Scab" stage of the disease was again forwarded from 10 different counties, but 6 of these constituted new records for perithecia, namely counties Mayo, Monaghan, Meath, Dublin, Kilkenny, and Waterford. Reports received along with the specimens, stated that the disease was not nearly so virulent along the western seaboard as in the previous year. The disease was reported from Co. Kilkenny as present in about 60 per cent. of the wheat crops, but the damage was not serious; and in Co. Cavan it was reported as occurring in almost every crop of the variety Queen Wilhelmina. These two counties are particularly mentioned as being those from which the disease was reported as being most prevalent.

Poor brairds, followed naturally by thin stands due to bad germination of infected grain and to "Seedling Blight," undoubtedly reduced yields in some cases. However, apart from these, and notwithstanding the general occurrence of infection in many wheat crops at harvest time, there was no record of any serious reduction in yield due to the "Ear Blight" and "Scab" stages of the fungus, such as occurred in 1942. This was borne out by examination of infected heads. With one exception, the grain in even the worst diseased heads was well developed, and although traces of pink-coloured grains were obvious in many harvested crops, shrivelling of grains was almost negligible, and germination was not seriously impaired by the amount of infection present.

The only other cereal forwarded with *G. Saubinetii* on it in 1943 was barley, a single sample being received which was badly infected with the perithecial stage of the fungus. This is the first record of "Scab" on barley in Ireland.

The Occurrence of *Gibberella Saubinetii* on Cereals in 1944.

Only one case of "Seedling Blight" caused by *G. Saubinetii* was identified in the spring of this year, the affected specimens being received from Co. Monaghan.

Through the continued co-operation of the Department of Agriculture, suspected specimens of cereals were again forwarded for examination. These included 92

samples of wheat, 20 samples of oats and 2 of rye. Considering the wheat first, 63 samples of this cereal were found infected with *G. Saubinetii*, 45 of these having the *Fusarium* stage only but the other 18 showed "Scab" in addition. On these scabbed specimens the perithecia, while well developed and mature, were not nearly so numerous as on infected heads in the two previous years. At the same time, wheat ears with perithecia were received from 9 counties; Co. Donegal being added to the existing records. This brings up to 17 the total number of counties from which perithecia have been recorded during the past three years. In the case of the oats, 8 of the 20 samples were infected with *G. Saubinetii*, 5 of them showing the "Ear Blight" stage only, and the other 3 having perithecia in addition. The two samples of rye showed only the *Fusarium* stage of the fungus.

Although samples of cereals were received from 17 counties in 1944, infection with *G. Saubinetii* was only detected on specimens from 12 of these counties. It was found that in cases where "Ear Blight" only was present on wheat heads (*i.e.* the conidial stage of the fungus), perithecia could be induced to develop in many cases by simply cutting the attached culms to a length of 6 inches and standing these with their cut ends in water in an open glass beaker, the heads projecting slightly above the mouth of the vessel. Where this was done at ordinary room temperature perithecia often developed, not however on the ears but on the stems just above the surface of the water.

Varieties of Wheat found infected by *G. Saubinetii* in 1943 and 1944.

Queen Wilhelmina	58 crops	Yeoman	2 crops
Atle	14 ,,	Pajbjerg	2 ,,
Red Marvel	9 ,,	Squarehead's Master	1 ,,
Diamant	6 ,,	Flygia	1 ,,
April Red	4 ,,	Not named	24 ,,
Manitoba	4 ,,		

Crop Preceding diseased Wheat.

Previous cropping and seed treatments before sowing are shown by the following data in so far as these details were supplied in the two years for affected crops:

Potatoes	30 fields.	Oats	14 fields.
Mangels and Sugar beet	7 ,,	Barley	1 ,,
		Lea	6 ,,
Other roots	15 ,,	No details	45 ,,
Wheat	7 ,,		

Seed Treatment before sowing.

Agrosan	4 crops.	Mercurial dusts, unspecified	10 crops.
Ceresan	8 ,,		
Carbosan	3 ,,	Copper sulphate	9 ,,
Coversine	2 ,,	Copper carbonate	1 ,,
Harvesan	1 ,,	Tar	1 ,,
Golden Grain	1 ,,	No treatment	38 ,,
Farmer's Friend	1 ,,	No information	46 ,,

Climatic Conditions in 1943 and 1944.

The spring in both these years was abnormally dry. Thus in 1943 rainfall for the month of February was only 0·99 inch and for March 0·72; in 1944 the relative figures were 1·19 and 0·30. Precipitation for April each year was also very low, see accompanying data on rainfall. These figures refer to Co. Dublin, but similar drought conditions were general throughout the country. Both of these dry springs were followed by dull cloudy summers, with just a little more sunshine for the months of July, August, and September, than in 1942, this increase being 10 hours in 1943 and 6 hours in 1944. Fortunately, in both years a spell of relatively dry weather coincided with the flowering of the wheat and the subsequent soft dough stage. The result of this was that climatic conditions were not favourable for the fungus at the most critical period of the host's growth. Hence, although the disease was prevalent enough in many crops towards harvest, there was no serious reduction in yield nor excessive shrivelling of grain in either year, such as occurred in the epidemic of 1942 (4).

The number of days on which precipitation occurred, and rainfall for each month, April to September inclusive, are shown at four separate stations in 1943 and 1944.

Month	Glasnevin, Co. Dublin (East Coast)		Ballyhaise, Co. Cavan (North Midlands)		Athenry, Co. Galway (West Coast)		Clonakilty, Co. Cork (South Coast)	
	No. of days	Rainfall inches	No. of days	Rainfall inches	No. of days	Rainfall inches	No. of days	Rainfall inches
April, 1943 ...	16	1·07	11	1·55	9	1·22	9	2·01
May, ,, ...	16	4·10	19	3·16	15	3·47	16	4·77
June, ,, ...	17	2·10	21	3·65	18	3·93	18	3·03
July, ,, ...	15	1·58	14	2·88	15	2·81	13	2·73
August, ,, ...	21	2·53	25	6·30	25	6·43	24	3·51
September, ,, ...	24	2·57	21	2·72	26	2·95	20	3·33
Totals ...	109	13·95	111	20·26	108	20·81	100	19·38
April, 1944 ...	14	1·69	8	2·11	10	1·82	13	3·26
May, ,, ...	10	0·92	14	2·15	11	3·23	9	0·98
June, ,, ...	16	1·46	18	2·38	17	3·01	12	1·12
July, ,, ...	20	2·37	22	3·86	23	4·50	20	4·22
August, ,, ...	16	2·61	15	3·51	21	3·41	13	1·92
September, ,, ...	18	5·56	19	4·31	17	4·15	18	4·98
Totals ...	94	14·61	96	18·32	99	20·12	85	16·48

Investigations on "Seedling Blight" at the Albert Agricultural College.

Experiment 1.—In the spring of 1943 wheat grain obviously infected with *G. Saubinetii* was mixed with healthy grain, and sown in pots of sterilized soil in an unheated greenhouse. No plants developed from any of the infected grains. Evidently this diseased seed was too thoroughly permeated by the fungus to germinate. On the other hand, all the healthy grains gave rise to normal plants, and there was no evidence of any spread of the fungus in the soil from the diseased grains to the healthy plants.

Experiment 2.—On the 6th April a nine-day-old culture of *G. Saubinetii* was mixed with the top two inches of sterilized soil in pots. These pots were sown with 240 grains of Queen Wilhelmina wheat which had been surface sterilised for five minutes in mercuric chloride solution 1/1,000, and then rinsed in sterile water. The pots were kept in an unheated greenhouse. The emergence of the plants from the soil was irregular, twelve days after sowing 208 plants had appeared, and at the end of three weeks the final number was 232. Of these, 60 were weak and chlorotic, and 2 dying. The latter succumbed inside the next week through basal decay, and the majority of the chlorotic plants showed a similar decay of the lowest leaf sheath, with a tendency for the rot to pass into the crown of the plant. When some of these plants were pulled up, the root system was found to be poorly developed and rotting, Fig. 1, Plate 1. Six weeks after sowing the number of chlorotic plants was 64, and 4 more had died after reaching a height of 2½ inches. These four were affected by severe root rot. The two seedlings which had first succumbed were now found *in situ* to have well developed perithecia of *G. Saubinetii* on their dead tissues above ground. Figs. 1 and 2, Plate 1, and these were exuding ascospores by the middle of June. Incubation in a humid atmosphere of the remaining dead specimens induced perithecial development here also in about a month. Measurements of the perithecia found on these seedlings showed them to be somewhat smaller as a rule than those formed on the glumes (4), the maximum being 219 x 175μ, minimum 175 x 131μ, with an average of 197 x 146μ.

No further dying of young plants occurred. The weak chlorotic individuals recovered and grew away more or less from the disease, but later in the season the fungus *G. Saubinetii* was obtained readily enough from dark brown areas in their outer leaf sheaths near the soil level. These plants were subsequently badly attacked by mildew, *Erysiphe graminis*, and quite a number of tillers failed to produce heads and died prematurely. Examination of these dead tillers in the month of October revealed their basal parts to be completely rotted, and numerous perithecia of *G. Saubinetii* present just above ground. In addition, on other tillers there were a few heads which failed to produce any grain, the ears being bleached and resembling those of plants attacked by *Ophiobolus graminis*. This failure may have been caused by the severe attack of mildew concurrently with the rather restricted root run of the plants, but it may be significant that occasional perithecia of *G. Saubinetii* were found on the base of these unproductive culms.

Appropriate controls sown in uninoculated sterilized soil and kept under similar conditions remained free from *G. Saubinetii* throughout.

Experiment 3.—Another attempt was made to induce "Seedling Blight" under glasshouse conditions by sowing 60 grains of Pajbjerg and 60 of Desprez in pots of sterilized soil. In this case the grain was sown on the 10th June and the soil in the pots then sprayed with a suspension of ascospores of *G. Saubinetii*. Germination of the grain was quick and growth of the plants at this time rapid. No "Seedling Blight" developed. These plants also became attacked by *Erysiphe graminis*, and after they reached the height of 24 inches the pots were placed on the floor of the greenhouse, where they remained until the end of the season. Prior to being thrown out in October an examination of the base of the plants showed that quite a number of them had developed perithecia of *G. Saubinetii*, although no signs of disease due to this fungus had been noticed previously.

Experiment 4.—This was an endeavour to produce "Seedling Blight" outside. Two hundred grains of each of the varieties Atle, Pajbjerg, and Queen Wilhelmina, were steeped for half an hour in a suspension of ascospores of *G. Saubinetii*. These contaminated grains were sown outside in the month of July. After sowing, but before the grain was covered with soil, it was also sprayed with the spore suspension. The plants appeared rapidly and grew away vigorously. Again there was no "Seedling Blight" nor any visible appearance of infection with the fungus. At heading out however, on comparing the inoculated row of Atle with its control row alongside, it was seen that, although the number of tillers in each was approximately the same, the number of heads in the former was considerably less than in the control. By the end of September some of the tillers in the inoculated row had died, their bases being rotted. The death of these tillers could not with certainty be attributed to *Gibberella Saubinetii*, but when the basal portion were incubated in a moist chamber perithecia of this fungus developed and finally produced ascospores.

Does *Gibberella Saubinetii* Persist in the Soil?

A number of pots of soil from Experiment 2 above, in which wheat plants had developed "Seedling Blight" or basal rot in 1943, were kept. The diseased plants were cut off at soil level and the roots remained in the soil. In December 1943, the topmost inch of soil in these pots was loosened, disturbing the roots of the previous plants as little as possible. Healthy wheat grain of the variety Queen Wilhelmina was then sown in the pots. These were then divided into two batches, one of which was kept in an unheated greenhouse and the other in a heated glasshouse. The seedlings in the latter emerged ten days before those in the cool house. There was 99 per cent. germination, and all seedlings appeared without any trace of disease in 1944. The plants grew to maturity and produced heads well filled with grain, and at no time during the growth of these plants was there any symptom of disease. After harvesting the grain, the pots with their stubble were placed under the benches of the greenhouse, where they remained for two months. The bases of the plants were then examined but no trace of *G. Saubinetii* could be found.

The evidence obtained from this experiment indicates that soil which produced plants diseased with *G. Saubinetii* does not retain its infectivity until the following season, even though the remains of such infected plants have been added to it.

The reason for this may be the one suggested by Bennett (1), namely that under field conditions much *Gibberella*-infected material is rendered innocuous through competition with saprophytes.

The Relation of Anthers to Infection of Wheat Ears by *Gibberella Saubinetii* on var. Queen Wilhelmina.

In June 1943, heads of wheat growing in a greenhouse were sprayed with a suspension of ascospores of the fungus when the anthers were extruded, and were then covered with small flasks to maintain a moist atmosphere. Four days later a white woolly growth of the fungus was visible on a number of anthers, but no other part of the ear showed infection at this time. Ten days after inoculation, 12 out of the 14 sprayed heads showed symptoms of disease. In all cases the anthers were the first to show signs of infection, and the disease then appeared on the glumes, which turned pale and developed brown patches. Infection soon spread to the rachis, and then the whole head rapidly bleached. No grain developed in any of the infected spikelets, but some shrivelled kernels were found in neighbouring spikelets.

Similar inoculations were carried out on 17 heads which had not yet come into flower. A few of these heads showed extruded anthers on the day following inoculation, and three days later 3 heads had anthers with a good growth of mycelium, but infection of the glumes was not apparent. Ten days after inoculation 5 heads were visibly infected, but only in three cases was growth of mycelium as profuse as when the anthers were exposed at time of spraying. The number of infected heads did not increase, and those already diseased developed symptoms similar to what are described above.

In another experiment the anthers were removed before extrusion from 12 heads of wheat growing in the open. These heads were then sprayed with a suspension of ascospores, and immediately covered with small flasks. Other heads which were in flower on the same plants were similarly inoculated and covered but no anthers were removed. Dealing with the latter lot first, as in previous cases, the anthers showed infection before other parts of the flower, and the disease then developed on the glumes. Three weeks after inoculation mycelium was abundant on these ears, being faint pink in colour and bearing sparse fructifications of the *Fusarium* type along the basal edges of the glumes. These infected heads remained slender, ripened prematurely, and all of them developed definite " Ear Blight ". The only grain found in them consisted of a few shrunken kernels. In the case of the first lot, that of the emasculated heads, no definite evidence of infection could be obtained, and plump well-developed grains formed in the majority of the spikelets. From this experiment it would appear that the removal of anthers rendered the ears less liable to infection.

Emasculated and non-emasculated wheat heads growing in the open were also sprayed with a suspension of ascospores of *G. Saubinetii* but the heads were left uncovered. In neither case was there any development of " Ear Blight " up to the time of ripening. Similarly, when wheat heads both immature and almost ripe

growing in the greenhouse were sprayed with a suspension of ascospores and left uncovered no disease developed. Sufficient moisture was evidently not present in these cases to ensure infection.

Spread of "Ear Blight" from Diseased to Healthy Wheat Ears by Contact.

In the month of August ten bundles of healthy wheat heads with stems 15 inches long were collected, all of these bundles were nearly ripe with the exception of the variety Atle, which was green at the time of collecting. Six of these bundles had heads of wheat badly infected with *G. Saubinetii* placed in their centre, and each bundle was tied so that it resembled a small sheaf. The bundles were then placed side by side on a bench in the laboratory. Four of those containing diseased heads and two without such heads were sprayed frequently with water for a period of three weeks, two bundles without diseased heads and two containing diseased ears being left unsprayed. When the bundles were opened and examined at the end of 45 days the following were the findings:

Bundle 1. Var. Atle.—Heads green and in flower when diseased ears were placed in the bundle; kept sprayed with water. A number of originally healthy heads in contact with diseased ones became infected and bound together by a weft of mycelium. No grain was formed in either affected or unaffected heads.

Bundle 2.—Heads ripe at time of inoculation; kept sprayed. A number of heads on contact with diseased ones were joined to them by a mycelial weft, but this was less profuse than in Bundle 1. Some of the grains in the newly-attacked heads were infected by the fungus.

Bundle 3.—Heads slightly green, grain well formed at time of inoculation, kept sprayed. Heads which were in contact with diseased heads attacked, and grains in affected portions of these heads shrivelled.

Bundle 4.—Heads nearly ripe, grain well formed at time of inoculation; kept sprayed. No infection developed on healthy heads even when in contact with diseased ones. Variety Desprez.

Bundles 5 *and* 6.—Uninoculated heads kept sprayed developed no symptoms.

Bundles 7 *and* 8.—Heads inoculated and kept dry developed no infection from diseased ears.

Bundles 9 *and* 10.—Heads uninoculated and kept dry developed no infection.

Discussion.

Some investigators believe that a relatively high soil temperature is necessary for the development of "Seedling Blight" of wheat (2 & 3). Bennett (1) however has shown that it can develop at a low soil temperature, particularly when environmental conditions are unfavourable for the host. The occurrence of "Seedling Blight" naturally in the spring of 1943 confirms Bennett's work. This phase of disease caused by *Gibberella Saubinetii* was reported mainly from sowings of wheat

made from February onwards. Two factors were probably involved in the prevalence of the disease in wheat sown at this time when compared with earlier sown crops (*i.e.*, autumn sown) These are, first, the best wheat is usually harvested and threshed early, and this grain is available and largely used for autumn sowing, whereas inferior crops are not threshed until later, and more infection is liable to be present. The second factor was climatic conditions, wheat brairds suffered badly from harsh dry weather in 1943, and this favoured the disease.

Grain which was obviously infected by *G. Saubinetii* failed to grow even under the most favourable conditions in a greenhouse. It is probable, therefore, that plants affected by "Seedling Blight" in the field only arise from grain which is slightly infected.

Under experimental conditions in the greenhouse with grain sown in contaminated soil in April, the percentage of plants killed by "Seedling Blight" was low. Conditions for growth at this time were good, and it is reasonable to assume that many more affected plants would succumb under more adverse conditions. This is actually borne out by field observations. Plants which are killed by the fungus in the seedling stage are a potential source of infection for the standing crop later on, as perithecia are produced on their dead tissues, and these fructifications may be liberating ascospores by the time wheat comes into flower. Under favourable climatic conditions many plants which are attacked by "Seedling Blight" may grow out of the disease more or less. Such plants are also a potential source of "Ear Blight," because infection is still present on the base of the culms, and in addition to causing dead or sterile tillers, perithecia may be formed.

A high atmospheric humidity is requisite for the development of "Ear Blight," and if such coincides with the flowering period of the host, then the greatest damage occurs. The fungus grows freely on the anthers as Pugh *et al* (5) have pointed out. As the wheat ripens the ears become more resistant to the disease, but infection may occur in stooks if sufficient moisture is present. Abundant moisture is also essential for the formation of perithecia, and the prevalence of these fructifications during 1943 and 1944 is attributed to the wet seasons. The importance of moisture for the development of perithecia is illustrated by their production on culms of wheat ears affected by "Ear Blight," when they are kept standing in water, and also by their formation on dead seedlings and tillers of affected plants.

Summary.

As a sequence to the epidemic of *Gibberella Saubinetii* in 1942, a considerable amount of infected grain was used for seed purposes the following season, none other being available. This resulted in a number of cases of thin brairds due to bad germination of the seed and to "Seedling Blight".

"Seedling Blight" was produced experimentally under glasshouse conditions, by sowing wheat in sterilized soil inoculated with a pure culture of *G. Saubinetii*. Plants killed by "Seedling Blight" are a potential source of infection to the standing crop as they may produce perithecia. Similar fructifications may be formed on the base of plants which recover from "Seedling Blight" attacks.

" Ear Blight " and " Scab " were both rather prevalent on wheat in 1943 and 1944. The approximate percentage of affected crops showing perithecia each year was 58 and 28 respectively. No serious reduction in yield nor shrivelling of grain took place in either year as climatic conditions favoured the host at its most critical period, and the fungus attacks occurred late in the season.

Explanation of Plate 1.

Fig. 1.—Wheat seedlings variety Queen Wilhelmina showing various stages of " Seedling Blight," obtained by adding a pure culture of *Gibberella Saubinetii* to sterilized soil before sowing. Note: perithecia are already developing about half way up on second seedling from right.

Fig. 2.—Enlarged view of perithecia of *G. Saubinetii* on dead tissues of young plant killed by " Seedling Blight " (× 6).

Fig.3.—Healthy control plant showing well-developed root system, the same age and kept under the same conditions as plants in Fig. 1, but grown in uninoculated soil.

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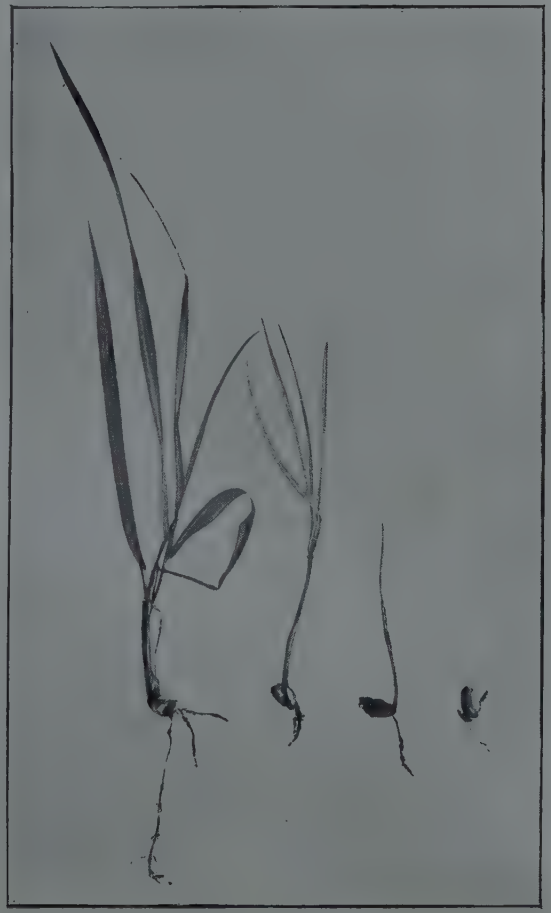

Photos by Fig. 1.

Fig. 2.

Fig. 3. [G. H. McLean.

No. 3.

CONTRIBUTIONS TOWARDS AN UNDERSTANDING OF THE CALCICOLE AND CALCIFUGE HABIT IN SOME IRISH PLANTS.

By

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The problem of the explanation of the calcicole and calcifuge habit in plants is still, in spite of the large amount of attention it has received, largely unsolved. A number of theories have been put forward, each with some evidence in its favour, but it is uncertain to what extent they should be regarded as mutually exclusive and to what extent as complementary; and it is also possible that the various factors suggested may in some cases operate simultaneously on the same plant, whereas in other cases different species in the same community may find themselves affected by different features of the same environment. The experiments and observations described below do not profess to form anything more than a small contribution towards the solution of this complex problem; and we would wish our results to be regarded as suggestive rather than conclusive. But their publication at this stage is, we feel, warranted by two considerations: firstly, that whereas most recent work has centred on the analysis of the calcifuge habit we have devoted more attention to calcicole species, and it is in relation to them that the more interesting results have been obtained; and secondly, that hitherto no study of the problem has been made with specific reference to Irish species and to the physico-chemical conditions that obtain in Irish soils.

General Considerations.

It must be explained at the outset that the words "calcicole" and "calcifuge" are here used in a purely descriptive sense. A calcicole plant is one which, under normal and natural conditions, is rarely or never found growing except in a soil that contains calcium carbonate in considerable quantities; a calcifuge plant one which, under normal and natural conditions, is rarely or never found growing except in a soil that is virtually free from calcium carbonate. The terms are in no way intended to beg the question whether or not the calcium content of the soil is in itself the critical factor; and though for some species the terms "silicicole" or "oxyphil" may be justified as alternatives to "calcifuge" they are, in the present state of our knowledge, not so well suited to a general discussion of the problem.

The chief points in which calcareous soils differ from non-calcareous ones, and which may, therefore, be of importance in determining the calcifuge or calcicole habit, are as follows:—

(i) *Alkalinity.*—The pH of calcareous soils in this country is usually between 7·0 and 8·5; that of non-calcareous soils usually between 4·0 and 6·5. There

is no evidence in the literature to suggest that a moderate degree of acidity is in itself injurious to calcicole species. On the other hand it has been claimed by Mevius (1924) for *Sphagnum spp.*, and by Rayner (1921) for *Calluna vulgaris*, that these calcifuge species require an acid medium for healthy growth. Pearsall (1922, 1926) however, who has found the latter species growing naturally on neutral gravels, disputes this conclusion.

(ii) *Higher calcium content.*—Many acid soils contain very little available calcium ; and De Silva (1934) has shown that certain species which possess a rather irregularly calcicole habit will flourish on any soil, no matter what its acidity, if the available calcium content is high enough. This interpretation of the calcicole habit has also been suggested by Truog (1918), Lundegardh (1924), and others. It has also been suggested that calcifuge species are adversely affected by a high concentration of calcium, which interferes with the absorption of potassium or magnesium (see Salisbury, 1920).

(iii) *Lower basic ratio.*—According to Pearsall (1922, 1926) and Pearsall and Wray (1927) neither acidity nor a low calcium concentration in absolute units is as important for calcifuge species as is a high ratio of univalent cations ($Na^{\cdot} + K^{\cdot}$) to bivalent ($Ca^{\cdot\cdot} + Mg^{\cdot\cdot}$). This ratio is, of course, normally high in acid, and low in calcareous soils.

(iv) *Precipitation of the sesquioxides.*—The amount of iron and aluminium in solution in the water of an acid soil is often considerable ; in a calcareous soil it is very small. This arises directly from the difference in pH, and also, in the case of iron, from the oxidation in calcareous soils (which have usually a much higher redox potential than acid ones) of ferrous to the much less soluble ferric hydroxide. It has been held, therefore, that calcicole species are those that are especially susceptible to aluminium poisoning, and that calcifuge species are those that have an unusually high iron requirement.

(v) *Lack of organic toxins.*—Whether peaty soils and the waters derived from them contain soluble organic compounds that are, quite apart from the acidity with which they are usually associated, toxic to certain species, is still a very vexed question. But it is possible that this may be a factor which prevents calcicole species from growing on certain acid soils.

(vi) *Higher nitrogen content.*—Calcareous soils are usually richer in nitrates than are non-calcareous : see Salisbury (1920), and Lundegardh (1931) for references. It has been suggested therefore that some calcicole species are really nitrophiles.

(vii) *Physical factors.*—In the British Isles most calcareous soils are better drained, and therefore drier, warmer, and better aerated than non-calcareous ones. In Ireland this contrast is of great importance, since the calcicole flora is best developed on the limestone pavements of the west and the eskers of the central plain—both of them environments which are, compared with the rest of the country, exceptionally well drained. Certain apparent calcicoles may, therefore, really be dry-soil plants.

In any attempt at an experimental analysis of the calcicole and calcifuge habits it is of course desirable to dissociate as far as possible the influence of these several factors. But this problem presents, unfortunately, grave difficulties. It is necessary to realize that whereas some of these factors are accidentally, and therefore separably, associated with alkalinity of the soil, others are inevitable concomitants of it. To the former category belong (vi) and (vii), and it is relatively easy to eliminate their influence in experimental cultures. The same is true of (v) if it is supposed that the toxins act independently of the acidity ; but authors are not agreed on this point, and as there seems to be little reliable information on the matter we shall not further consider this factor.

Factors (i) to (iv), on the other hand, cannot be completely dissociated from differences in acidity. It is possible to prepare acid soils in which the calcium content and the basic ratio vary within wide limits ; and also, if water cultures be used, to vary the concentration of dissolved iron and aluminium in an acid medium. But to bring about the corresponding variation in an alkaline soil or solution is impossible. If any substance other than calcium carbonate is used to maintain the alkalinity new and disturbing factors are introduced ; and calcium carbonate inevitably means plenty of calcium in solution and a high basic ratio. Moreover the sesquioxides are inevitably precipitated by a rise in pH, no matter what the composition of the medium.

While we claim, in the experiments described below, to have largely eliminated factors (vi) and (vii), no attention has been paid to (iv) or (v). In some of the experiments a partial dissociation of (ii) and (iii) from (i) has been attempted.

EXPERIMENTAL CONDITIONS.

Plants belonging to 22 species that are, in Ireland, either calcicole or calcifuge were grown from seed in pots or boxes in a cool greenhouse. Two series of cultures were made of each species ; these differed from one another in one particular only—the amount of calcium carbonate in the soil. Care was taken to see that in all other physical and chemical conditions, as well, of course, as in the origin and quantity of the seed sown, the two series of cultures were identical. In some cases only a single sowing on each soil-type was made ; in other cases the sowings were duplicated or triplicated. But in either event the results presented here represent the average result given by a considerable number of seedlings, whether grown in the same box or not—a number large enough to eliminate the effects of fortuitous genetic variation in the material. The species discussed below all gave reasonably consistent results ; the rather inconsistent results given by three other species have been omitted.

The seed was collected from wild plants growing in their most typical environment. In all cases seed from several separate individuals was mixed together, and later distributed at random among the different cultures.

The basis of the artificial soils used for the experiments was a peat-sand mixture which consisted of 22% (by weight) of air-dry peat and 78% of sea sand, freed from calcium carbonate by treatment with acid. For some of the experiments the sand was supplemented by debris derived from well-weathered granite. Both the peat and the granite debris presumably contained small quantities of soluble mineral matter, but since the aim of the experiments was to control only the supply of calcium carbonate, and to provide an adequate supply of all other nutrients, this has no bearing on the comparative results presented here.

The peat-sand mixture served without further addition as the soil for the non-calcareous cultures. For the calcareous cultures calcium carbonate was added in the form of a mixture of equal parts of precipitated calcium carbonate powder and coarsely ground oyster shells. In most of the experiments enough of this mixture was added to form 13·3% of the weight of the air-dry soil; but for those species numbered (4), (5), (6), (9), (10), (13), (14) and (21) in the list below, only half this quantity (i.e. 6·7% of the total weight) was used. In either case the soil was distinctly alkaline; the change was made because it was felt that the conditions provided by the larger proportion of calcium carbonate were perhaps rather too extreme. They can, nevertheless, be matched in many natural soils.

A stock nutrient solution was made up; it contained 0·13 M calcium nitrate, 0·29 M potassium dihydrogen phosphate, 0·35 M magnesium sulphate, and traces of iron, copper, zinc, manganese and boron. This was diluted 40 times before use. It was given every one or two weeks, in quantities determined by the rate of growth of the plants; but the same quantity was, of course, given on each occasion to all the cultures of any one species. All plants were given water as required, the only criterion being the appearance of the soil. They were thinned as soon as this became necessary to prevent serious over-crowding.

The pH of the non-calcareous soil (i.e., the peat-sand mixture with nutrient solution) was about 5·2, that of the calcareous soil about 8·0.

In some of the experiments the cultures in non-calcareous soil were duplicated: one series was given the nutrient solution just described, the other a similar solution but with the calcium nitrate replaced by an equivalent of sodium nitrate. The purpose of these experiments was to assess the importance for growth in an acid soil of a plentiful calcium supply.

The following species of plants were grown:—

CALCICOLES.

(1) *Geranium lucidum* L.
(2) *Carlina vulgaris* L.
(3) *Blackstonia perfoliata* Huds.
(4) *Origanum vulgare* L.
(5) *Juncus inflexus* L.
(6) *Verbascum thapsus* L.
(7) *Hypericum perforatum* L.
(8) *Leontodon hispidus* L.
(9) *Poterium sanguisorba* L.
(10) *Aquilegia vulgaris* L.
(11) *Reseda luteola* L.
(12) *Centaurea scabiosa* L.
(13) *Erigeron acer* L.
(14) *Antennaria dioica* Gaertn.
(15) *Leontodon taraxacoides* Lac.

CALCIFUGES.

(16) *Juncus squarrosus* L.
(17) *Radiola linoides* Roth.
(18) *Senecio sylvaticus* L.
(19) *Jasione montana* L.
(20) *Digitalis purpurea* L.
(21) *Rumex acetosella* L.
(22) *Lepidium heterophyllum* Benth.

In these lists the species have been arranged in groups, in accordance with the extent to which the calcicole or calcifuge habit is strongly or feebly developed. Thus (1) to (3) are very strongly calcicole, and (14) and (15) only feebly so; similarly with the calcifuge species. Within each group the order is arbitrary. The necessary data for this grouping has been derived from *Cybele Hibernica* (2nd edition), Scully (1916) and Praeger (1933), supplemented by field observations. This gradation in the intensity of the calcicole or calcifuge habit should be borne in mind in interpreting the results given below.

RESULTS.

(*a*) *Total failure.*—In only three cases did a plant completely fail to establish itself on one of the soils. *Blackstonia* failed on the non-calcareous, and *Juncus squarrosus* and *Radiola* on the calcareous soil. In all cases the seeds germinated normally, but the seedlings made no progress, and died within a fortnight of germination.

All these instances of failure are, naturally enough, of plants grown on the type of soil on which they are never found wild. But the case of *Blackstonia* is peculiar, since, as will be seen below, all the other calcicole species did well on non-calcareous soil. It is possible that the exceptional behaviour of this species may be connected with its mycorrhizal habit.

(*b*) *Difference in the rate of germination.*—In species (1) and (2) germination was much slower (by 6–12 days) on the calcareous than on the non-calcareous soil. This is striking in view of the particularly pronounced calcicole habit of these species. The same delaying effect of calcareous soil was shown to a lesser extent in species (6), (16) and (17).

Borthwick (1936) found that calcium, even in quite small concentration, delays germination in *Hypericum perforatum*, apparently by diminishing the permeability of the testa. In our experiments with this species germination was simultaneous on all soils, but it is probable that in none of them was the concentration low enough to bring about the rapid germination obtained by Borthwick in distilled water.

(*c*) *Difference in the percentage of seeds germinating.*—In species (1), (11) and (12) among the calcicoles, and (16), (18), (19) and (20) among the calcifuges, the number of seeds that ultimately germinated was significantly lower on the calcareous than on the non-calcareous soil. That this phenomenon should be shown by four out of five of the pronouncedly calcifuge species is not surprising: that it should be shown also by three calcicoles is less expected. The percentages of the seeds of these species (*Geranium lucidum*, *Reseda luteola* and *Centaurea scabiosa*) that ger-

minated on calcareous and non-calcareous soil respectively are as follows: 37% and 75%; 43% and 69%; 33% and 54%.

Only one species (*Hypericum perforatum*) showed a significantly higher percentage of germination on calcareous soil. In the remaining species the percentage germinating on the two soils was almost identical.

(*d*) *Pathological symptoms.*—In four species culture on calcareous soil produced symptoms that may fairly be described as pathological, in contrast to the normal appearance presented by the plants grown on non-calcareous soil. Two of these species were calcicole and two calcifuge. In *Reseda luteola* a chlorosis of the leaf-margins appeared about three weeks after germination, but after a further two weeks it disappeared. In *Centaurea scabiosa* the growth and geotropic response of the radicle seemed to be deficient on calcareous soil, with the result that most of the seedlings were not adequately rooted in the soil during their first few weeks. In the calcifuge species, *Senecio sylvaticus* and *Jasione montana*, the symptoms were not so definite, but for about a month the seedlings on calcareous soil looked extremely miserable, and at any time throughout this period their death would not have been surprising. A considerable proportion of the *Jasione* seedlings did, in fact, die, but the remainder ultimately made a fair recovery, as did almost all those of *Senecio sylvaticus*.

(*e*) *Different growth-rate in early stages.*—The most general result of the experiments is the smaller growth-rate of almost all the species on calcareous soil. *Blackstonia*, as has already been mentioned, failed completely on the non-calcareous soil. Two other calcicole species—*Origanum vulgare* and *Poterium sanguisorba*—showed throughout the course of the experiment identical behaviour on the two soils. But the remaining 19 species, calcicole and calcifuge alike, all showed slower growth in their early stages on the calcareous soil. In accordance with their later behaviour these species can be divided into four groups:—

(i) Those in which the plants on calcareous soil never recovered from this initial handicap and were still, after 6 or 12 months, very much smaller than the plants on non-calcareous soil. To this group belong species (2) and (14) (calcicole), and (19) and (21) (calcifuge), as well, of course, as the two calcifuge species mentioned earlier which completely failed on the calcareous soil.

(ii) Those that showed a partial, but not complete recovery from the initial handicap. To this group belong species (8) and (18).

(iii) Those in which the plants on calcareous soil recovered completely in the later part of the experiment, so that at the end they showed no significant differences from the plants grown on non-calcareous soil. To this group belong (5), (10) and (12) (calcicole), and (20) and (22) (calcifuge).

(iv) Those in which the recovery was more than complete—that is to say in which the plants on calcareous soil were at first smaller, but ultimately larger, or stronger and healthier than the others. It must be emphasized, however, that this reversal, though unmistakable, was in no case dramatic; for in all species the plants

on non-calcareous soil remained reasonably healthy and well-developed throughout. To this group belong species (1), (6), (7), (11), (13) and (15), all calcicole.

A few quantitative data may be given here, to illustrate in greater detail the behaviour of species in each of these four groups; to avoid repetition only one species will be selected from each group. C indicates calcareous, and NC non-calcareous soil; the dates indicate the time after sowing. The measurements indicate, of course, average dimensions, not those of any one plant.

(i) *Carlina vulgaris.*—6 weeks: C, plants 14 mm. across, with 2 leaves; NC, plants 27 mm. across, with 3-4 leaves. 10 weeks: C, plants 20 mm. across, with 3-4 leaves; NC, plants 50 mm. across, with 6-7 leaves. 26 weeks: C, 33 mm. across; NC, 100 mm. across. 54 weeks: C, 55 mm. across; NC, 140 mm. across.

(ii) *Senecio sylvaticus.*—6 weeks: C, 26 mm. across, with 4 leaves; NC, 59 mm. across, with 7-8 leaves. 13 weeks: C, 65 mm. high; NC, 115 mm. high. Both are coming into flower. 24 weeks: C, 175 mm. high, with average of 29 capitula; NC, 210 mm. high, with average of 37 capitula.

(iii) *Centaurea scabiosa.*—7 weeks: C, plants with 2 leaves, the longer 36 mm. long; NC, plants with 4 leaves, the longest 62 mm. long. 9 weeks: C, plants with 4 leaves, the longest 56 mm. long; NC, plants with 6 leaves, the longest 74 mm. long, and considerably broader than the leaves in C. 17 weeks: Equal; plants in both series have average of 10 leaves. 26 weeks: Still equal.

(iv) *Reseda lutevla.*—6 weeks: C, 48 mm. across, with 6 leaves; NC, 74 mm. across, with 9 leaves. 9 weeks: C, 95 mm. across; NC, 110 mm. across. 10 weeks: Equal. 13 weeks: plants in C slightly larger than in NC, and with more leaves in healthy condition. 26 weeks: C, 220 mm. across; NC, 170 mm. across, and with fewer leaves.

There remain to be considered those experiments, referred to above, in which the plants on acid (non-calcareous) soil were divided into two groups, one being supplied with a good ration of calcium and the other with hardly any. The results of these experiments were somewhat inconclusive, and they need not be given in detail. It is sufficient to say that in none of the species tested did the substitution of sodium nitrate for calcium nitrate in the nutrient solution have a significantly adverse effect on the growth of the plants. It follows that at any rate a number of calcicole species are able to thrive on a very low calcium supply (which was presumably derived mainly from the Dublin tap-water—not a rich source). It is of interest to note that Marsden-Jones and Turrill (1938) found that *Anthyllis vulneraria*, a moderate calcicole, when grown on soil in which no calcium whatsoever could be detected by the ordinary analytical methods, not only flourished, but yielded on incineration an ash with a remarkably high calcium content.

It does not, of course, follow that some species may not, as was suggested by De Silva (1934), owe their calcicole habit to a high requirement of available calcium in the soil. Some of our own observations suggest that in Ireland this may well be true of *Arum maculatum*, *Tussilago farfara*, and perhaps *Origanum vulgare*. But for the majority of calcicole species some other explanation must be sought.

Discussion.

It would appear from these experiments that a calcareous soil is, in comparison with a mildly acid one, an unfavourable environment for seedlings not only of calcifuge, but also of many calcicole species. This somewhat unexpected conclusion is supported by the general facies of the calcicole flora, whether on chalk down, on esker, or on limestone pavement. All three communities have, in greater or less degree, a characteristic and attractive appearance, which is due to the dwarf habit of most of the plants. As soon as one moves away on to ordinary, neutral grassland one is struck by the rankness of the vegetation. Similarly, if species such as *Carlina vulgaris* or *Erigeron acer* are grown in garden soil, they develop with a startling luxuriance which renders them almost unrecognizable to the field botanist who has seen only the stunted specimens that the esker soil produces. Little is known of the behaviour of calcicole species when grown under controlled conditions with a known pH ; but it is significant that Olsen (1921) found that the optimum pH for many indifferent species was well on the acid side of neutrality, and scarcely higher than the optimum for other species that are strongly calcifuge. It would appear that alkalinity is almost universally deleterious.

How then is the calcicole habit to be accounted for ? Primarily, it would appear, on a basis of differential susceptibility. Calcicole species are those which, although adversely affected in their early development by calcareous soil, are less seriously affected than are the majority of indifferent or calcifuge species, and are thus given a competitive advantage. It is, of course, well known that competition can play a very important part in determining the habitat of a plant ; the classical examples are *Achillea moschata* and *A. atrata* in Central Europe, and *Galium sylvestre* and *G. saxatile* in the British Isles. (For the latter, see Tansley, 1917.) In both cases it has been shown that, while under natural conditions the first species of the pair is strictly calcicole and the second strictly calcifuge, either will grow under artificial conditions on either type of soil, if it is protected from competition. The habit of the species is determined under natural conditions by differential survival on each type of soil. Our experiments would seem to suggest that the same factor is at work in determining the calcicole habit of many Irish species ; for the fact that these species grow as well, and sometimes better, on acid soils when given the chance indicates that it is only competition from indifferent and calcifuge species that denies them a foothold on these acid soils under natural conditions.

The results of our experiments on calcifuge species present, in themselves, no difficulty ; for all prospered, to a greater or less extent, better on non-calcareous than on calcareous soil. But the similarity in the general course of the experiments on *Senecio sylvaticus* and *Digitalis purpurea* to those on calcicole species shows how exceedingly delicate must be the balance of factors involved in successful competitive survival in determining whether the habit be calcicole, calcifuge or indifferent. *Digitalis purpurea*, for example, is, in the broad features of its distribution, one of the most reliable of calcifuge species ; and yet the only effect of a calcareous soil on its growth is to produce a temporary check no worse than that suffered by many calcicole species. It is perhaps significant that in its occasional,

sporadic appearances in limestone districts it is usually to be found in small pockets of soil on bare rock (as on the limestone mountains of Co. Sligo) or in earth-filled chinks in walls. One of us has found it in the latter situation near Killarney, in a pocket of soil of which the pH was 7·0. The same wall harboured, in other pockets with the same, or even lower pH, the strongly calcicole species *Geranium lucidum* and *Ceterach officinarum*. This tendency to occur on limestone soils in crannies where there is no continuous carpet of competing vegetation suggests that if the intensity of competition were even slightly reduced the distribution of the species might be much more widespread.

It is necessary, when considering the adverse effect of the calcareous soil on the calcicole species, to realize that it has two very different aspects. The production of pathological symptoms, or of apparently permanent dwarfing, does without doubt take place in some species; and this must represent in all circumstances a very real handicap to the plant in question. But in many other instances the chief effect of the calcareous soil seems to be a delaying one; the seedlings grown on it are, on a given date, smaller and more backward than those grown on the non-calcareous soil, but they represent simply a stage through which the latter have passed some days or weeks before. Now a delay of this kind in early development would clearly be fatal to a seedling that was attempting to compete with others which are not susceptible to the same effect, and were showing normally rapid growth. But if, as would seem probable, all the plants which grow on a highly calcareous soil experience the same effect, then the time factor becomes of no consequence, and the healthier growth ultimately shown on calcareous soil in our experiments by such species as *Geranium lucidum*, *Hypericum perforatum* and *Reseda luteola* may help to determine their calcicole habit.

In conclusion, we must briefly consider the connexion, to which allusion has been made earlier, between the dryness of a soil and its calcium carbonate content. Brenchley (1912) found that certain weeds of arable land that are calcicole in Somerset and Wiltshire are indifferent, or even calcifuge, on the drier soils of E. Bedfordshire; and several species that are markedly calcicole in Ireland are indifferent in S.E. England. But none of the calcicole species dealt with in this paper can be explained purely as dry-soil plants, for their distribution is very different from that of species such as *Hieracium vulgare* or *Linum catharticum* which, though they are most abundant on the calcareous soil of the eskers, are also very common on acid soils wherever the drainage is good enough. But it may be that for some species the two factors—true calcicole habit and preference for dry soils—reinforce each other, and thus restrict the distribution of the species in Ireland more rigidly to calcareous soils than the effect of the chemical factor alone would warrant. *Carlina vulgaris*, for example, is generally speaking a very strict calcicole in Ireland, but it is fairly frequent on steep, sandy and gravelly banks in Glendalough and Glenmalure which are quite free from calcium carbonate (Praeger, 1933, and personal observations). It would seem probable that this species is really a dry-soil plant and also a moderate calcicole; but that the scarcity of well-drained non-calcareous soils in Ireland transforms it effectively into a strict calcicole.

Summary.

Twenty-two species of plants, of which fifteen are calcicole in their Irish distribution, and seven calcifuge, have been grown from seed under identical conditions in two artificial soils, one containing calcium carbonate, the other free from it.

In general the calcareous soil was found to have an adverse influence on both calcifuge and calcicole species. Of the calcicoles, *Blackstonia perfoliata* failed completely on the acid soil, *Origanum vulgare and Poterium sanguisorba* showed similar behaviour throughout on the two soils, and the remaining twelve were at some period of their growth (usually in the seedling stage) adversely affected by the calcareous soil. In nine species this initial handicap was later made up, and the plaints on the calcareous soil eventually made as good (in six species, slightly better) growth as those on the acid soil. Of the calcifuge species, *Radiola linoides and Juncus squarrosus* failed completely on the calcareous soil; the others were adversely affected by it, on the whole more severely than were the calcicole species; but there was, in their cultural behaviour, no clear-cut division between the two groups.

It is suggested that the calcicole habit must be largely determined by differential survival in an environment that is universally unfavourable; but that the balance between environmental and competitive factors must be exceedingly delicate in determining whether the habit be calcicole, calcifuge, or indifferent. The significance of the dryness of most calcareous soils is discussed.

No evidence was obtained to suggest that, in any of the species selected for experiment, the concentration of available calcium in the soil is *per se* a major factor in influencing distribution.

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No. 4.

THE ANGULAR DISTRIBUTION OF SUBMARINE DAYLIGHT IN DEEP WATER.

By

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A number of workers have studied the angular distribution of daylight beneath the surface of the sea or of lakes. In particular, Johnson and Liljequist (4) have made many measurements beneath the surface of Swedish fjords, using a photometer sensitive only to a narrow cone of rays, and adjustable in direction so as to enable polar curves of the illumination to be plotted for any desired vertical plane. Most of their curves refer to sunlit conditions with a smooth water surface. In general they found that the increased extinction of oblique rays caused the obliquity of the maximum radius vector of their curves to decrease with increase of depth, the curves usually becoming relatively less elongated at the same time.

There does not appear however to be any decisive evidence in favour of a decrease in the vertical extinction coefficient such as would accompany a decrease of average obliquity with increase of depth. In fact, for monochromatic light in homogeneous water, the coefficient appears to vary little with change of depth in unsheltered waters where the obtaining of such polar curves would be very difficult. Lack of homogeneity will of course affect the coefficient one way or the other, and the use of too wide a spectral band will cause it to decrease owing to the filtering-out of the less penetrating wave-lengths. Moreover, in measurements made by Atkins off Plymouth (1) no correlation has ever been found between the vertical extinction coefficient at depths exceeding 20 metres and either the degree of roughness of the surface or the nature of the daylight, whether entirely diffuse or low or high sunlight.

This suggests that the average obliquity tends to a constant value governed by a balance between the opposing effects of absorption and scattering, one decreasing and the other increasing the obliquity with increase of depth. Some evidence in support of this view is furnished by measurements of the ratio of the horizontal to the vertical illumination made by Atkins in 1938–1939 (2). These failed to show any regular change with depth in the ratio horizontal/vertical.

Johnson and Liljequist's results were mostly obtained nearer the surface, where the distribution was evidently largely governed by that of the daylight above, but even in their case it is not obvious that the broadening of their curves with increase of depth does not off-set the reduction in obliquity of their major axes, so that the average obliquity may be little affected.

EQUILIBRIUM DISTRIBUTION ON THE ASSUMPTION OF SPHERICAL SCATTERING.

It may be of interest to consider the distribution to which we should expect the balance between absorption and scattering to lead, and to see how far it can be reconciled with the experimental results. The problem of the contribution made by scattered light has been theoretically considered by Le Grand (6), and by Whitney (8). These authors deal chiefly with moderate depths, at which the scattered light forms so small a part of the whole that multiple scattering may be neglected. They both assume as an approximation that the light scattered by the diffusing material in any small element of volume is equally distributed in all directions, regardless of the direction of the incident light.

This simplifying assumption is also made below. It would be true if the scattering were due solely to reflection by polished spherical particles large compared with the wave length, but, in making it for sea water in order to make the mathematics manageable, we must remember that our only justification is the large variation likely to occur in the sizes and natures of the particles in suspension, some large compared with the wave length, causing a preponderance of backward irregular reflection if opaque or of forward transmission if transparent, others comparable in size with the wave length giving a distribution varying with their diameters, the intensity being a minimum perpendicular to the incident light for very small particles. Le Grand (*loc. cit.* p. 404 *et sec.*) gives an account of these effects, and shows that in sea water scattering by the molecules is generally small compared with that by particles in suspension.

Let us suppose that a parallel beam of monochromatic radiation of flux F, in passing through a thin perpendicular layer of sea water of thickness dx, loses by absorption and scattering $cFdx$, of which a fraction $scFdx$ is due to scattering in all directions, the remainder being due to absorption. We may call s, i.e. the fraction of the total extinction that is due to scattering, the 'scattering fraction.'

Suppose that direct sunlight falls on a smooth water surface at such an angle that its refracted path in the water makes an angle α with the vertical. Let the intensity of illumination on a surface perpendicular to the beam just below the surface be I_0 lux (i.e. lumens per sq. metre). Then at a depth x the intensity *of the direct sunlight* will be $I_0 e^{-cx\sec\alpha}$, but, even if we suppose that there is no diffuse sky light, the vertical intensity recorded by a horizontal photometer will, in general, not fall off according to the exponential law, as the relative importance of the vertical component of the scattered light will increase with the depth. This effect is considered quantitatively by Le Grand, who, however, deals chiefly with the upper layers where the contribution of the scattered light is so small that doubly scattered light may be neglected. In what follows we are concerned with the lower layers in which equilibrium angular distribution has been reached. It is evident that this cannot occur until all the light has been scattered at least once.

If the water is deep enough we may, for the levels in which we are interested, neglect reflection off the bottom. The illuminations at two points P and Q will have the same angular distribution and only differ by a factor depending on their difference in level. If that at the upper point P is multiplied by any number that at Q will be multiplied by the same number, since the latter is due solely to the illumination

passing downward through the P level. Hence it is easily seen that once equilibrium has been reached the vertical extinction of the diffuse light follows an exponential law. This would generally not be true near the bottom, where reflected light would cause a variation in the angular distribution with depth.

Let us adopt the following notation, using the metre, the lux, and the lumen, as units of length, intensity of illumination, and flux.

c=Coefficient of extinction (including absorption and scattering) for a parallel beam.

s=Scattering fraction, i.e. fraction of the total light removed from a beam that is due to scattering (the rest of the loss being due to absorption). It is assumed that this scattering is equally distributed in all directions.

μ=Coefficient of vertical extinction attained at depths at which the angular distribution has reached equilibrium.

$k=\mu/c$.

J=Total flux per sq. metre of diametral cross section received by a spherical photometer from the lower hemisphere. The diametral cross section is evidently $1/4$ of the total area of the photometer.

K=Total flux similarly received from the upper hemisphere.

$L=J+K$=total or integral flux per sq. m. at the point considered, i.e. the illumination effective in causing photo-synthesis.

U=Flux per sq. m. received on a horizontal plane photometer facing downwards (i.e. upward vertical illumination in lux).

V=Flux per sq. m. received on a similar photometer facing upwards (i.e. downward vertical illumination in lux, as commonly measured).

H=Flux per sq. m. of vertical diametral section received by a cylindrical photometer with its axis vertical. The diametral section is evidently $1/\pi$ of the curved vertical surface of the photometer.

B=Brightness of field in lux per steradian as viewed from the photometer. The brightness in lamberts will be $\pi B \times 10^{-4}$

In every case the photometer surface is assumed to absorb in accordance with the cosine law.

Since equilibrium has been attained and the angular distribution is constant the ratios $J : K : L : U : V$ are independent of the depth; each of these quantities decreasing exponentially with a vertical extinction coefficient μ, i.e. kc.

We shall in future consider these quantities as referring to the point O, the position of the photometer.

Let PQ in Fig. 1 be an element of volume in the form of a thin slab of the medium of area A and thickness dx exposed to parallel illumination of intensity I

lux (as measured on a perpendicular photometer) falling on the slab at an angle of obliquity a. The element will scatter $IA \cos a . s \operatorname{sec} a . dx$ i.e. $Iscdv$ lumens, where dv is its volume. As this is independent of a the flux scattered by a volume element exposed to total illumination L from all directions will be $Lscdv$. We assume that this scattering takes place equally in all directions, as indicated in the figure, so that the volume element acts as a source of intensity $Lscdv/4\pi$ candle power.

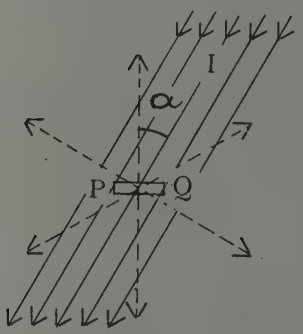

Fig. 1.

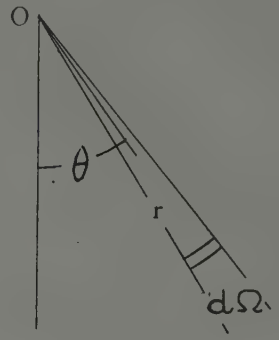

Fig. 2.

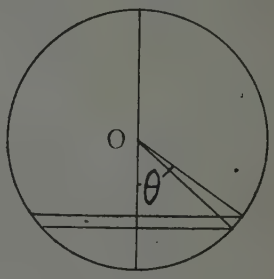

Fig. 3.

Consider the brightness of field B in a direction making an angle θ with the downward-drawn vertical through O (see Fig. 2). Evidently, considering the illumination received at O from a small solid angle $\delta\Omega$ in the given direction, we have

$$B\delta\Omega = \int_0^\infty \frac{scLe^{-\mu r \cos\theta}}{4\pi} \cdot r^2 \delta\Omega \cdot \frac{e^{-cr}}{r^2} \cdot dr$$

$$\text{so } B = \frac{scL}{4\pi} \int_0^\infty e^{-(1 + k\cos\theta)cr} dr$$

$$\text{or } B = \frac{sL}{4\pi(1+k\cos\theta)} \qquad (1)$$

where L is now the total illumination at O, provided that $1+k\cos\theta$ is always positive, i.e. that $k<1$. We shall find that this condition is satisfied for all possible values of s, but that if the latter is small k is very close to unity. This would imply that equilibrium is only reached at great depths.

It is interesting to note that on the assumption of spherical scattering the vertical extinction coefficient μ is always less than the extinction coefficient for a parallel beam c, the contribution made by the scattered light more than offsetting the increased extinction due to obliquity.

Equation (1) shows that the equilibrium polar surface of brightness of field is an ellipsoid of eccentricity k, O being the lower focus. As k would generally be not much less than unity the ellipsoid would be much elongated.

Integrating over a sphere as indicated in vertical section in Fig. 3 we find

$$L=\int_0^\pi B\ 2\pi \sin\theta\, d\,\theta = \frac{sL}{2}\int_0^\pi \frac{\sin\theta\, d\,\theta}{1+k\cos\theta}$$

$$=\frac{sL}{2k}\log\frac{1+k}{1-k}$$

$$\therefore\ s=\frac{2k}{\log\frac{1+k}{1-k}} \qquad (2)$$

The logs being to the base e.

This shows the relation between s and k. Evidently if $s=0$ (no scattering) $k=1$, equilibrium only being reached at an infinite depth where absorption has rendered the light purely vertical. As s increases k decreases, thus justifying our assumption that $k<1$. If s is near unity (absorption small) k is small, the conditions approximating to those obtaining in a thick cloud. Values of k for different values of s are plotted in Fig. 4.

Dividing L into its lower and upper parts we have

$$J = \frac{sL}{2}\int_0^{\pi/2}\frac{\sin\theta}{1+k\cos\theta} = \frac{sL}{2k}\log(1+k) \qquad (3)$$

$$\text{and } K = \frac{sL}{2}\int_{\pi/2}^{\pi}\frac{\sin\theta}{1+k\cos\theta} = \frac{sL}{2k}\log\frac{1}{1-k} \qquad (4)$$

We are generally more interested, however, in U and V, the illuminations recorded by down- and upturned plane photometers.

$$\text{We have } U = \int_0^{\pi/2} B2\pi\sin\theta\cos\theta d\theta = \frac{sL}{2}\int_0^{\pi/2}\frac{\sin\theta\cos\theta d\theta}{1+k\cos\theta}$$

$$\text{Hence (see Appendix A) } U = \frac{sL}{2}\cdot\frac{k-\log(1+k)}{k^2} \qquad (5)$$

$$\text{Similarly } V = -\int_{\pi/2}^{\pi} B\ 2\pi\sin\theta\cos\theta\, d\,\theta$$

$$\text{so } V = \frac{sL}{2}\cdot\frac{\log\frac{1}{1-k}-k}{k^2} \qquad (6)$$

To measure the horizontal component of the illumination we would need a vertical cylindrical photometer surface exposing the same effective area to light from all azimuths.

$$\text{Evidently } H=\int_0^\pi B\ 2\pi\sin^2\theta d\theta = \frac{sL}{2}\int_0^\pi \frac{\sin^2\theta d\theta}{1+k\cos\theta}$$

Hence (see Appendix B) $$H = \frac{\pi s L(1-\sqrt{1-k^2})}{2k^2} \qquad (7)$$

From (5) and (6) we get $$\frac{U}{V} = \frac{k-\log(1+k)}{\log\frac{1}{1-k}-k} \qquad (8)$$

from (7) and (6) $$\frac{H}{V} = \frac{\pi(1-\sqrt{1-k^2})}{\log\frac{1}{1-k}-k} \qquad (9)$$

(3), (4), (2) and (6) give $$\frac{J}{V} = \frac{k\log(1+k)}{\log\frac{1}{1-k}-k} \qquad (10)$$

$$\frac{K}{V} = \frac{k\log\frac{1}{1-k}}{\log\frac{1}{1-k}-k} \qquad (11)$$

and $$\frac{L}{V} = \frac{k\log\frac{1+k}{1-k}}{\log\frac{1}{1-k}-k} = \frac{2k^2}{s(\log\frac{1}{1-k}-k)} \qquad (12)$$

(3) and (5) give $$\frac{J}{U} = \frac{k\log(1+k)}{k-\log(1+k)} \qquad (13)$$

Several workers have made measurements of U/V, which is generally a few per cent. A few measurements have been made of H/V, those by Atkins in 1938–9 being around 80 per cent. L/V is of interest as showing the ratio of the photosynthetic activity of the light to the vertical illumination as usually recorded. K/V measures the mean obliquity of the downward-travelling light, while J/U gives the corresponding obliquity for that travelling upwards.

For values of k not exceeding 0.99 (for which $s=0.375$) it is convenient to assume values for k and hence from (2) and (8) to (13) find the corresponding values of s and the ratios U/V etc., as plotted in Fig. 4. For values of k very close to unity it is more convenient to use approximate formulae, taking assumed values of s. In this case

(2) becomes $$\log\frac{1}{1-k} = \frac{2k}{s} - \log(1+k) = \frac{2}{s} - 0{\cdot}693 \text{ nearly}$$

(8) ,, $$\frac{U}{V} = \frac{0{\cdot}307\,s}{2-1{\cdot}693\,s}$$

(9) ,, $$\frac{H}{V} = \frac{\pi s}{2-1{\cdot}693\,s}$$

(10) ,, $$\frac{J}{V} = \frac{0{\cdot}693\,s}{2-1{\cdot}693\,s}$$

(11) becomes $$\frac{K}{V}=\frac{2-0\cdot693\,s}{2-1\cdot693\,s}$$

(12) ,, $$\frac{L}{V}=\frac{2}{2-1\cdot693\,s}$$

(13) ,, $$\frac{J}{U}=\frac{0\cdot693}{0\cdot307}=2\cdot26$$

Also $$\frac{H}{U}=\frac{\pi}{0\cdot307}=10\cdot2$$

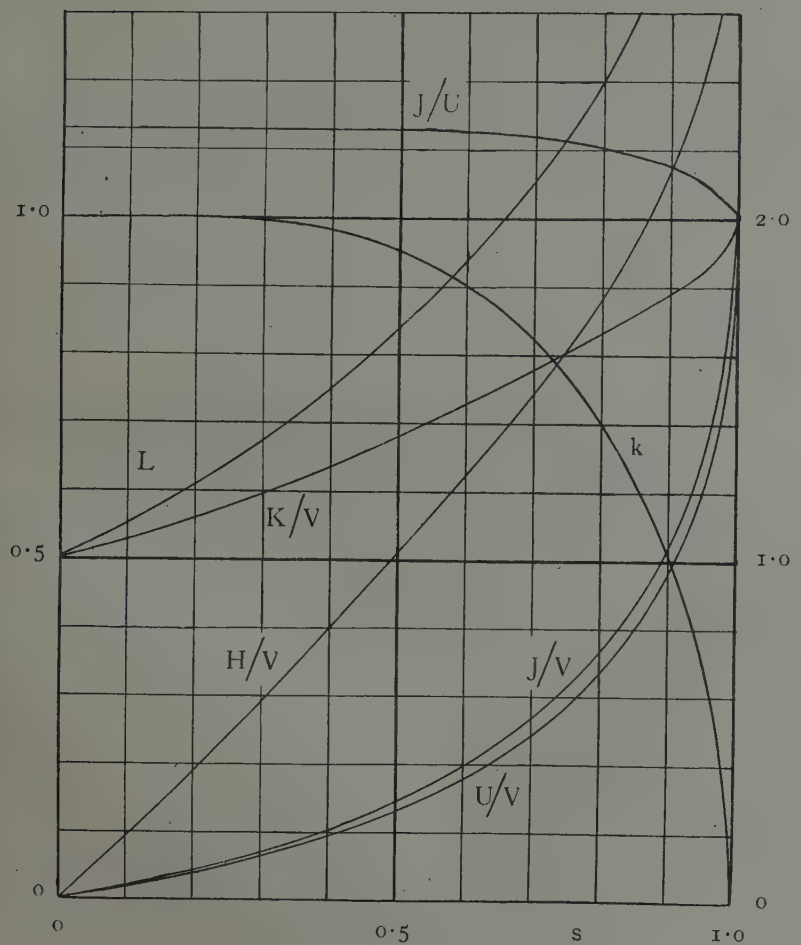

Fig. 4.

These approximations may be made for values of s up to 0·3, which corresponds to $k=0·9975$. It is worth noting that for these small values of s the average obliquity of the upward-scattered light is almost constant, and may be represented by $\sec^{-1} 2·26$, i.e. nearly 64°, while the horizontal light recorded by a cylindrical photometer is about 10 times the upward light. We shall find later that this theoretical result for the ratio H/U does not seem to be borne out by experience.

The ratios found from equations (2) and (8) to (13) are plotted against s in Fig. 4, k and U/V in accordance with the scale on the left, the remainder on the half scale shown on the right.

A number of measurements of U/V have been made, notably by Utterback (6) in the Pacific, Clarke (3) in the Western Atlantic, and Atkins (1) in the English Channel. A few measurements of H/V have also been made, of which those made by Atkins are considered here. From the experimental values of U/V or from those of H/V we can read from the figure the corresponding values of s and of the other ratios on the assumption of equilibrium distribution and spherical scattering, and thus if U/V and H/V are measured simultaneously we can test the assumptions made.

We see from the figure that as s rises from 0 to 1, L/V rises from 1 (purely vertical light) to 4 (perfectly diffuse light), K/V, the mean secant of the obliquity of the downward light, rises from 1 to 2, and J/U, the mean secant of the obliquity of the upward light falls from an almost stationary value 2·26 to 2·00. It may be noted that the upward light is always more oblique than the downward, so that the ratio U/V under-rates its photosynthetic importance. The fall of k, i.e. μ/c, with increasing s in spite of the increasing obliquity shows the great importance of scattered light in reducing the vertical extinction.

Comparison with Experimental Results.

We may compare the above results with some measurements made with a cubical photometer by Atkins off Plymouth in 1938–39. (2). These gave simultaneous values of U/V and H/V. Unfortunately the few series were only of a preliminary nature, further work being prevented by the outbreak of war.

The results are shown in the table, in which the series are arranged in order of decreasing values of U/V, which only makes one slight deviation from decreasing order of μ. Percentages are used for convenience in printing.

Table.

Series	μ %	U/V %	$U/\mu V$ %	s %	H/V %	s^1 %	s^1/s
C 1	20·0	5·50	27·5	27·5	—	—	—
C 5	13·5	3·45	25·6	18·9	84	42	2·22
C 4	11·5	3·17	27·6	17·6	80	40	2·28
C 3	11·0	3·02	27·5	16·9	73	37	2·19
C 6	11·2	2·98	26·6	16·7	81	40	2·39
C 7	7·6	2·10	27·6	12·3	80	40	3·25

C 1 and C 6 .. Low Sun. Strong Wind.
C 7 .. .. High Sun. Strong Wind.
C 5, C 4 and C 3 .. Overcast. Very Light Wind.

It has been pointed out by J. G. Moore (private communication) that, as shown in the 4th column, $U/\mu V$ is almost constant. There does not, however, appear to be any evident theoretical justification for this relation beyond the qualitative one that as s is small in pure water it will naturally tend to increase with the amount of matter in suspension, so that both μ and U/V will increase together. In finding the values of s given in the table use was made of the approximate form of (8) which is applicable to the low values concerned, and gives more accurate results than could be read from the figure.

No values are shown for H/V for Series C1, which was made with the ship anchored inside Plymouth breakwater with strong sunlight, as rotation of the photometer rendered the interpretation of the results difficult. The mean values for depths of 10 m. and over for the other series are shown, and the corresponding values, s^1, of the scattering fraction, as read from the curve. On our assumptions s^1/s should equal unity, instead of being around two or three.

No very great weight can be attached to these few results which were obtained under conditions which were not ideal, especially as trouble was experienced with the photo-cells, whose sensitivity fell considerably in the course of a few months. Moreover, in Series C 6 and C 7 the combination of bright sun, strong wind, and rough sea, rendered the determination of H/V difficult, and the interpretation of the results uncertain. The sun was low in C 6 and high in C 7, but in both cases the rough surface with breaking waves must have rendered the average obliquity comparatively large just below the surface, and there was no obvious difference in the recorded mean values of H/V. It was evident in both series that even at 40 m. equlibrium distribution was far from being attained, as at that depth the illumination on a vertical surface perpendicular to the sun's azimuth exceeded the mean for other azimuths by about 20 per cent. in C 6, and as much as 48 per cent. in the clearer water of C 7.

They are, however, the only simultaneous measurements of U, V, and H with which I am acquainted. Earlier comparisons by various workers in which the photometer was successively suspended at different angles can hardly be regarded as very satisfactory, owing to possible changes in the conditions in the interim, or to possible differences in depth owing to variations in the rate of drift of the ship. Utterback's early simultaneous measurements of U and V (7) were made with a photometer without diffusing glass, and sensitive only to a comparatively narrow angle. They naturally gave smaller values for U/V owing to the greater average obliquity of the upward light.

The results, for what they are worth, suggest very strongly that the ratio H/U is two or three times as great as would be expected on the assumption of uniform scattering. Even though equilibrium had not been attained the absence of any tendency of either U/V or H/V to change regularly with depth seems to imply that their values were close to the equilibrium ones. We shall see below that the values found for H/V are also close to those to be expected just below a calm surface illuminated by a uniform overcast sky.

The greater part of H is supplied by zones somewhat above the horizontal, for which the average total scattering (much of it multiple) is through angles from 45° to 90°, whereas U is mainly due to light which has been scattered through

angles from 135° to 180°. It would appear, therefore, that single scattering through comparatively small angles is considerably greater than that through angle exceeding 90°.

This is the exact opposite of the diffuse reflection that would be produced by unpolished particles large compared with the wave length, nor does it agree with the true scattering by particles very small compared with the wave length. The latter is just twice as large for angles near 0° or 180° as for 90°, the distribution being symmetrical about the 90° plane.

The effect might be produced by refraction through comparatively large transparent particles, or by true scattering by particles comparable with the wave length (see Le Grand *loc. cit.*, p. 407).

It is evident from the figure that the values of U/V recorded give values of k only very slightly less than unity, while for the values of H/V k is about 0·985. This would imply that angular equilibrium would only be attained at great depths if the scattering were uniform (see derivation of equation 1). As we have seen, however, there is evidence that the scattering through small angles exceeds that through large, which would hasten the attainment of equilibrium. We could not, of course, expect the polar surface to be ellipsoidal.

Although it would appear that, owing to the nature of the scattering particles, the theoretical results given above do not apply quantitatively to sea water, it would appear to be reasonable to draw some qualitative conclusions from them. Thus from equation (8) we see that U/V is a function of k, and hence of s only, and not an explicit function of μ. This should still be true even if the scattering is not uniform if we interpret s as a measure of light scattered through large angles. The colour of the upward scattered daylight therefore depends only on the variation of s with wave length. In ocean water the total extinction is a minimum in the blue in spite of the fact that, in the comparative rarity of particles in suspension, molecular scattering, which is inversely proportional to the fourth power of the wave length, must add appreciably to the total scattering in that spectral region. The decrease in extinction is due to reduced absorption by the water, which is most transparent in the blue. Increased scattering and reduced absorption combine to raise s and hence U/V. As the molecular scattering increases with reduction in wave length we should expect the maximum value of s to occur deeper in the blue than the region of maximum transmission. Thus ocean water looks a deeper blue than the colour for which the transmission is greatest. Further inshore the maximum transmission shifts towards the green. This can hardly be entirely due to increased scattering of the short waves by the greater number of particles in suspension, as if so the water would maintain its deep blue tint, whereas the maximum value of U/V is now in the green. It seems to be more probably due to absorption of the blue light, either by particles of a yellowish or greenish colour, or by a dye or stain in solution, as suggested by Kalle (5), which would, however, tend to reduce U/V. In turbid water almost all the extinction is due to the particles (except possibly in the red, where the water absorbs very strongly), and the colour is determined by that of the particles. If for them s is independent of the wave length the water will appear grey. See Le Grand *loc. cit.*, p. 429, and bibliography of earlier authors.

ANGULAR DISTRIBUTION JUST BELOW A CALM SURFACE.

It may be of interest to compare the values actually found for H/V with that to be expected just below a smooth water surface illuminated by a uniform overcast sky. We shall neglect the loss of light by reflection at the surface. This simplification will exaggerate the importance of light whose obliquity in the water is only slightly less than the critical angle 48·6°. The approximation will tend to allow for the effects of a slight ruffling of the surface, such as will almost always occur at sea under even the calmest conditions.

It is easy to show that the light just below the surface will be limited to a vertical cone of semi-angle γ equal to the critical angle, the brightness of field within the cone being n^2 times that of the sky, where n is the refractive index of the water. The brightness B is thus uniform over the cone.

Evidently $V=2\pi B\int_0^{\gamma} \sin\theta\cos\theta\, d\theta$

$$=\frac{\pi B}{2}(1-\cos 2\gamma)$$

and $H = 2\pi B\int_0^{\gamma}\sin^2\theta\, d\theta=\pi B(\gamma-\frac{\sin 2\gamma}{2})$

$$\therefore H/V=\frac{2\gamma-\sin 2\gamma}{1-\cos 2\gamma}$$

Taking n as 1·33 we find $\gamma=48\cdot6°$ and $H/V=0\cdot626$.

This, however takes no account of scattered light from the lower hemisphere. As U/V is never more than a few per cent., and as internal reflection from the surface is also small for angles within the critical angle, we may neglect the contribution of U to V. The contribution to H is, however, appreciable, as it includes the horizontal components, not only of the entire lower hemisphere, but also of the total reflection by the surface of that part of it lying beyond the critical angle. We can only make an approximate allowance for this contribution in view of the deviation between the theoretical and the experimental results for H/U. If, however, we assume as a value for s the mean of the results found from U/V in Series C 3, C 4, and C 5, i.e. 0·178, we shall at least get a fair value for the upward component of the lower hemisphere, and shall probably not grossly underestimate its horizontal component, since the greater part of the excessively high value of H/U found by measurement probably comes chiefly from the upper hemisphere (which is of course absent, as far as scattered light is concerned, just below the surface).

This value of s makes k very close to unity, the approximate form of (2) showing that $1-k=2e^{-2/s}$, which amounts to about 2×10^{-5}. This means that in

the integral given in Appendix B the term involving $\sqrt{1-k}$ only becomes appreciable when θ approaches π making $\tan\frac{\theta}{2}$ large. Thus it becomes a very simple matter to find the value of the integral for the whole lower hemisphere and add, for the reflected light, the value for the part outside the critical angle. When this is done we find that we should add 0·110 to the value of H/V to allow for the total effect of the lower hemisphere. This raises the theoretical value of H/V just below a calm surface to 0·726, an estimate which is probably slightly low.

We see then that the values actually found for H/V are not very different from those to be expected just below a calm surface illuminated by a uniform sky. The fact that no regular variation with depth was found in these values seems to indicate that they also approximate to the equilibrium value reached in deep water. The latter therefore seems, for the conditions under which these measurements were made, not to differ greatly from the value to be expected just below the surface. Further measurements are however very desirable.

Summary.

(1) Experimental results show little if any regular variation with depth in the vertical extinction coefficient or in the ratio of the horizontal to the vertical illumination, if the measurements are made for approximately monochromatic light in homogeneous water. The extinction coefficient seems to be only slightly affected by the state of the water surface or by the angular distribution of the daylight.

(2) This has led to the suggestion by more than one worker that the angular distribution, and hence the average obliquity, tend to be determined by a balance between the opposing effects of absorption and scattering, the first decreasing the mean obliquity and the second increasing it.

(3) An attempt is here made to present the theory of such an equilibrium distribution on the assumption that the scattering of a beam of light by the particles in suspension takes place equally in all directions. The polar surface of field brightness so found is an ellipsoid of revolution about a vertical axis, the point of observation being the lower focus.

(4) It is shown that, on this hypothesis, the equilibrium value of the vertical extinction coefficient is always less than the extinction coefficient (including all scattering) for a parallel beam. Where only a comparatively small part of the extinction is due to scattering the difference between the two coefficients is very small. This would mean that equilibrium would only be approached very slowly.

(5) Comparison of the theory with a few simultaneous measurements of the downward, upward, and horizontal illuminations made off Plymouth in 1938–1939 shows lack of agreement, the results apparently showing a considerable excess of scattering through angles less than 90°. This seems to indicate that the scattering is mainly due either to transparent particles large compared with the wave length or to particles comparable in size with the wave length.

(6) Although this discrepancy prevents the theory from being applied quantitatively to the conditions under which the measurements were made it would seem likely that some qualitative deductions may be drawn from it. Thus it shows that the ratio of the upward to the downward illumination (i.e. the albedo of the underlying water) depends only on the relative importance of scattering and absorption in producing extinction, and not directly on the total value of the extinction coefficient. This explains how the variation of the albedo with wave length and hence the colour of the water, may be expected to depend on the nature of the water.

(7) Measurements made at various depths below a comparatively calm surface with a cloudy sky gave a value for the ratio of the horizontal to the vertical illumination close to that to be expected just below the surface. The approximate constancy of this ratio as the depth increased indicated that it was also close to the equilibrium value reached in deep water. Further measurements are, however, very desirable.

APPENDIX.

A.

$$\int \frac{\sin\theta\cos\theta\, d\theta}{1+k\cos\theta} = -\frac{1}{k}\left[\cos\theta\log(1+k\cos\theta)+\int\sin\theta\log(1+k\cos\theta)\,d\theta\right]$$

$$= -\frac{1}{k}\left[\cos\theta\log(1+k\cos\theta)-\frac{1+k\cos\theta}{k}\left\{\log(1+k\cos\theta)-1\right\}\right]$$

$$= \frac{1}{k^2}\left[\log(1+k\cos\theta)-(1+k\cos\theta)\right]$$

Hence $$\int_0^{\pi/2}\frac{\sin\theta\cos\theta\, d\theta}{1+k\cos\theta} = \frac{k-\log(1+k)}{k^2}$$

and $$-\int_{\pi/2}^{\pi}\frac{\sin\theta\cos\theta\, d\theta}{1+k\cos\theta} = -\frac{k+\log(1-k)}{k^2} = \frac{\log\frac{1}{1-k}-k}{k^2}$$

B.

$$\int\frac{\sin^2\theta\, d\theta}{1+k\cos\theta} = \frac{1}{k^2}\int\frac{(1-k^2\cos^2\theta)-1+k^2}{1+k\cos\theta}\,d\theta$$

$$= \frac{1}{k^2}\int(1-k\cos\theta)\,d\theta - \frac{1-k^2}{k^2}\int\frac{d\theta}{1+k\cos\theta}$$

$$= \frac{\theta-k\sin\theta}{k^2} - \frac{1-k^2}{k^2}\int\frac{d\theta}{1+k\cos\theta}$$

$$\text{Now } \int \frac{d\theta}{1+k\cos\theta} = \int \frac{d\theta}{(1+k)\cos^2\frac{\theta}{2} + (1-k)\sin^2\frac{\theta}{2}}$$

$$= \frac{1}{1+k}\int \frac{\sec^2\frac{\theta}{2}\, d\theta}{1+\frac{1-k}{1+k}\tan^2\frac{\theta}{2}}$$

$$\text{Let } \sqrt{\frac{1-k}{1+k}}\tan\frac{\theta}{2} = \tan\varphi$$

$$\text{so } \sqrt{\frac{1-k}{1+k}}\sec^2\frac{\theta}{2}\,\frac{d\theta}{2} = \sec^2\varphi\, d\varphi$$

$$\text{Then } \int \frac{d\theta}{1+k\cos\theta} = \frac{2}{\sqrt{1-k^2}}\int \frac{\sec^2\varphi\, d\varphi}{1+\tan^2\varphi}$$

$$= \frac{2\varphi}{\sqrt{1-k^2}} = \frac{2}{\sqrt{1-k^2}}\tan^{-1}\left\{\sqrt{\frac{1-k}{1+k}}\tan\frac{\theta}{2}\right\}$$

$$\text{Hence } \int_0^{\theta} \frac{\sin^2\theta\, d\theta}{1+k\cos\theta} = \frac{1}{k^2}\left[\theta - k\sin\theta - 2\sqrt{1-k^2}\tan^{-1}\left\{\sqrt{\frac{1-k}{1+k}}\tan\frac{\theta}{2}\right\}\right]$$

The integral vanishing at the lower limit.

$$\text{So } \int_0^{\pi} \frac{\sin^2\theta\, d\theta}{1+k\cos\theta} = \frac{\pi\,(1-\sqrt{1-k^2})}{k^2}$$

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No. 5.

DEVELOPMENTAL LINES IN POLLINATION MECHANISMS IN THE CONIFERALES.

By

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Pollination, and its relation to ovular structure, have been described in a series of recent papers by Doyle and O'Leary (1935 a, b, c) and Doyle and Kane (1943). These papers have special reference to the Pinaceae, and, with the exception of two genera, the phenomena are now fairly clear in that family. Although detailed observations have still to be made in many genera of other families, yet, from the information already at hand about these, it seems possible and timely to offer suggestions concerning at least some of the lines along which modifications in pollination mechanisms may have taken place in the Coniferales as a whole, and to indicate also where information is particularly lacking. The tracing of these lines has been made feasible by recent extensions of our knowledge of Carboniferous and Permian conifers by Walton (1928) and particularly by Florin (1938–9, 1939).

It is to be emphasized that this paper is not concerned with problems such as the immediate phyletic relationships of individual living and fossil genera, but solely with the relationships between types of pollination mechanisms as far as these are known.

The Palaeozoic Types.

The sections at present available of Florin's monograph (1938–9) on Palaeozoic conifers provide details of the structure of the gynostrobilus, ovule, and pollen grain, of several species of *Lebachia* (the old genus *Walchia* in part). Other genera are considered in sections not available, but general features have been summarized in a preliminary note (Florin 1939). These ancient members of the Coniferales appear to be related to the better known Cordaitales, although not descended from them, the two groups representing two lines of descent from some still earlier phylum. It is thus of interest that the *Lebachia* species had a grain, and presumably also a pollination mechanism, similar to that of the Cordaitales, and that the grain definitely differed from that of the other large Palaeozoic order, the Pteridospermae (Florin 1937). It is then here assumed that some such type as that described for *Lebachia* is basal and primitive in the conifers.

The cone of *L. piniformis* shows a close series of spirally arranged bracts in the axils of most of which stands a fertile dwarf shoot (Fig. 1 A). This shoot has a number of sterile appendages, clearly reduced telomes, one of which carries a single

erect ovule. The extine of the pollen, Fig. 1 B, expanded into a large balloon-like air sac, *a*, covering the whole of the grain except for a small area at that part called by Florin the distal pole, *p*, corresponding in position to the furrow (cf. Wodehouse 1935) in modern grains. The Pteridospermae did not possess a balloon air sac, which was however characteristic of the Cordaitales (Florin 1936). Further, since the grains passed through the micropylar canal to lodge in the pollen chamber of the nucellus, it would seem that fluid must have been exuded from the micropyle, some type of pollination drop in which the air-borne grains were caught. The details of subsequent phenomena must naturally always remain obscure, but the structure

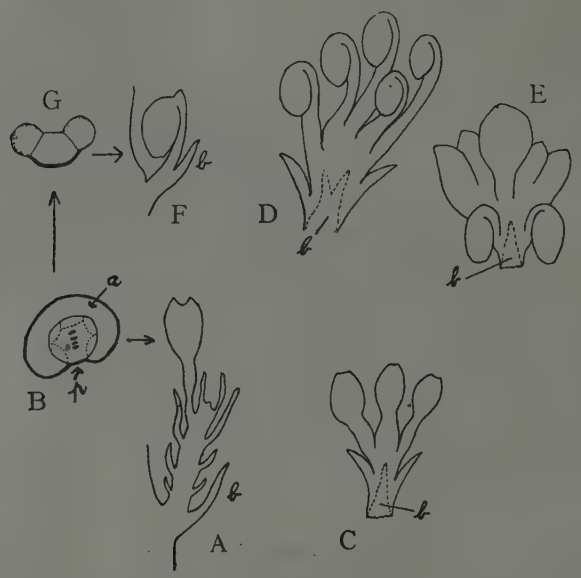

Fig. 1 Ovuliferous structures in Palaeozoic conifers (diagrammatic after Florin and Walton). A. *Lebuchia pinifomis*. B. Pollen of same; *a*, balloon air-sac; *p*, distal pole. C. *Ernestiodendron filiciforme*. D. *Walchia germanica*. E. *Pseudovoltzia Liebeana*. F. *Ullmannia Bronni*. G. Pollen of same. In each *b*=cone bract.

of the grains suggests that the air-sac round it was a flotation device of such a nature that the grain would tend to float with its distal pole, *p*, the probable position of germination, underneath. The slow or rapid reabsorption of the pollination fluid would cause the grain to be drawn into the pollen chamber orientated, at least roughly, with its germinating or fission area below. Florin's (1938–9, Heft 1) statement that the cones of *L. piniformis* are " stets ± aufrecht gestellt " supports this suggestion.

It may be taken as certain that some exudation of pollination fluid was a feature, not only of these early conifers, but of all the primitive gymnosperms, Cordaitales and Pterdospermae alike. It is still a feature of the living Cycadales, the Gnetales, and *Ginkgo*. It is also shown in all families of the living Coniferales

except the Araucariaceae, in which a specialized type of mechanism has been developed. An exudation of pollination fluid from the ovule is thus taken as basal in the Coniferales.

Many other types of these Upper Carboniferous and Permian conifers are known. Certain simple features of some of them are illustrated in Fig. 1, modified very diagrammatically from Florin (1939) and Walton (1928). All of them showed a cone, as in *Lebachia*, with a series of spirally arranged bracts, each bract carrying in its axil a special reproductive dwarf shoot. In each case, in Fig. 1, a single such shoot is outlined, either isolated, as in C, D, E, with the abaxial bract, *b*, dotted, or in relation to the bract and main cone axis, as in B, G. *Lebachia* with its single terminal ovule (1 A) has already been referred to. In other forms, notably species of *Walchiostrobus*, several of the telomic appendages on the reproductive shoot carried erect ovules, the shoot and its appendages tending to become broadened and flattened. This tendency is well expressed in *Ernestiodendron filiciforme* Florin, Fig. 1 C, in which the axillary fertile shoot became itself wholly flattened taking the form of a large lobed (*i.e.* branched and fasciated) ovuliferous scale. In others the ovules carried terminally on the units of such a condensed flattened branching system had become inverted. *Walchia germanica* Florin carried up to five such inverted ovules on distal units of the branching system, Fig. 1 D, while *Pseudovoltzia Liebeana* (Geinitz) Florin carried two (occasionally three) near the base, Fig. 1 E, recalling the structure of the ovuliferous scale of a member of the Pinaceae. In *Ullmannia Bronni* Goeppert the telome appendages and the axillary dwarf shoot are fused, the whole appearing as a fairly simple flattened scale which bears a single inverted ovule, Fig. 1 F. *Pseudovoltzia* and *Ullmannia* are Upper Permian, the others Lower Permian or Carboniferous.

Except for *Lebachia* accurate published details are not yet available concerning the pollen structure of most of these, although it would appear that the older forms with erect ovules showed the grain type already mentioned for *Lebachia* and shown in Fig. 1 B. With regard to the forms with inverted ovules *Ullmannia*, at least, had a pollen grain, Fig. 1 G, provided with two lateral air-sacs like a modern pine. This interesting fact was given in a personal communication from Dr. Florin, obtained through the kind co-operation of the Swedish Consul in Dublin, N. L. Jaenson, to whom a very sincere expression of thanks is due.

The existence in Upper Permian time of an inverted ovule pollinated by a grain with two lateral air-sacs is of great interest. It definitely demonstrates that there took place in the Permian, coupled with the ovular inversion, the change from the primitive grain of *Lebachia* to the modern type, a change simply effected by the suppression of the proximal part of the all-over balloon sac. Many intermediate forms probably existed, such as can be seen in more recent cases. Thus in *Abies nobilis* and *Podocarpus macrophyllus* (Wodehouse 1935), and in specimens of *Pinus silvestris* from certain post-glacial deposits (Florin 1936), there is shown, instead of two lateral sacs, a single bladder completely encircling the distal part of the grain, and intermediates may also occur. The occurrence of three lateral sacs is well known for *Pherosphaera* and *Microcachrys*, and has also been recorded in some species of *Podocarpus*. Many such variants, obvious derivatives from the *Lebachia* type, may have appeared among the Permian conifers with inverted ovules, and

it is here suggested that, when details are available, all the Upper Permian conifers with inverted ovules will prove to have had grains of some such type. It is obvious that these grain types are all merely form variants. They are simply grains provided distally with bladders and all probably function in the same manner. The air-sacs, causing the grains to float in the pollination fluid, facilitate their rise in it *upwards* through the micropylar tube of an *inverted* ovule. At the same time, since the bladders are expansions of the distal part of the grains, these will tend to rise, so oriented that the germinal furrow lies above ; thus the part of the grain which makes contact with the nucellus, or at least tends to lie nearest to its surface, is the part from which the pollen tube will later emerge. In the primitive forms with erect ovules, as *Lebachia*, the balloon sac covering a grain tends to keep it floating with the distal pole below, again keeping this area in relation to the nucellus. With ovule inversion the limitation of the air-sac to the distal zone of the grain has, in a very simple way, ensured the reversal of the flotation position of the pollen. The air-sacs seem then to be primarily flotation bladders, a point already emphasised in the account given of pollination in *Pinus* (Doyle & O'Leary 1935 b).

The view has been put forward by Wodehouse (1935) that the function of the lateral air-sacs, in say *Pinus*, is the protection of the germinal furrow on dessication. This view was expressed however before Florin's account of grain structure in the Cordaitales and the Palaeozoic conifers was available. *Lebachia*, for example, has no true germinal furrow, and here the balloon air-sac is solely a flotation device ; and in the grains of the two-winged type it is not clear why any such protection should be required in nature. The grains, maturing rapidly in the pollen sac, are spread immediately by wind, and are then either lost or come at once into contact with a moist ovule into whose micropyle they are quickly absorbed. Air-sacs on the pollen sacs, therefore, are taken to be primarily a simple flotation mechanism, although in some modern grains they may function secondarily as protection to the germinal furrow.

Apart from the value of these suggestions it is, at any rate, certain that some conifers of, at least, the Upper Permian had inverted ovules and two-winged grains ; and the pollination type, of which *Ullmania* is an example, leads directly to the mechanisms still shown in two of the modern families—the Pinaceae and the Podocarpaceae. Again it is not suggested that these two families necessarily arose from any of the known Permian genera. Ovule inversion and the development of a two-winged grain may not have been achieved by their immediate ancestors till the early Mesozoic. Nor do the extraordinary close similarities that exist between the pollination mechanisms in *Pinus* and *Podocarpus* necessarily mean that these are both to be traced to the same root ancestry. Such questions are not being considered here. But the point is quite definite that the *type* of pollination deemed basal in these two families is not a hypothetical one but one known to have been already developed in the phylum in Permian time and readily derived from a more primitive *Lebachia* type.

Acceptance of the *Lebachia* type of grain as primitive in the conifers, and the derivation from it of the modern two-winged form by reduction, involve naturally the acceptance of Florin's (1936, 1937) criticisms of Wodehouse's (1935) views on primitive grain types not only in the conifers but in the Palaeozoic gymnosperms

as a whole. It is unnecessary to repeat these criticisms here, but Florin's work shows that many of Wodehouse's statements are erroneous, based as they were on data which at the time were incomplete.

THE PINACEAE.

An inverted ovule, an exudation of fluid from the micropyle, and a two-winged grain or some variant of it, functioning as outlined above, are taken to be basal in this family. But within the family several important modifications of the basal type have occurred. There are to be seen, at least, (a) the *Pinus—Picea* type, (b) the *Picea orientalis* type, (c) the *Pseudotsuga—Larix* type, (d) the *Abies—Cedrus* type, (e) the *Tsuga Pattoniana* type, and (f) the ordinary *Tsuga* type. The mechanisms in *Pseudolarix* and *Keteleeria* have not yet been recorded, and are therefore omitted in the discussion which follows. They may prove different from those so far described. Within some of the larger genera minor differences have been described, and it is possible that a comprehensive examination of all the species might bring to light still other mechanisms or important variations on those here listed. But a broad analysis of those already known and described brings out features of much interest.

The types listed are related to four major modifications :—(1) loss of pollination exudate, (2) development of stigmatic devices eventually replacing the primitive method of pollen reception by this exudate, (3) reduction and eventual loss of the air-sacs from the pollen grains, and (4) pollen germination elsewhere than on the nucellus. Further, on various morphological grounds the members of the Pinaceae are often grouped in two series, one including *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*, and the other *Abies*, *Cedrus*, *Tsuga* (*Keteleeria*, and *Pseudolarix*). Each of these two series shows its own special line of modification in pollination mechanism, and in each case the line culminates in a type in which the four major factors are expressed. This can best be seen by a brief review of the salient facts of which the details have been fully recorded in the papers already cited (Doyle and O'Leary, 1935 b, c ; Doyle and Kane, 1943). The conclusions are summarized diagrammatically in Fig. 2. Here the two serial lines are based on the Upper Permian *Pseudovoltzia Liebeana*. This is given merely as a convenient and relatively well-known type, the plan of whose cone and ovuliferous scale resembles that in the Pinaceae. It is assumed that its pollination mechanism was that already taken as basal in the family. Its grain, as outlined in section in 2 *a*, could have been, immaterially, a cleanly two-winged form or one with a circular air-sac round the whole distal zone. In other words, Fig. 2 A is simply meant to represent in a general way what the ovule-bearing apparatus and the pollen grain in the ancestral *type* of the Pinaceae must have been like.

The *Pinus—Pseudotsuga* line, indicated to the left of Fig. 2 A, can first be followed.

A. The Pinus—Picea *type.* The pollination mechanism in these two genera seems closest to the basal *Ullmannia—Pseudovoltzia* type. The young cones stand rigidly erect so that the ovules are inverted, not only in relation to the cone axis, but in fact (2 B, *Pinus*, and 2 C, *Picea*), while the fluid exudate, suggested by the

dotted line across the micropylar canal in both B and C, and the characteristic two-winged grain 2 *p*, permit the typical flotation mechanism to be easily seen in operation. Both however have advanced beyond the primitive type by the

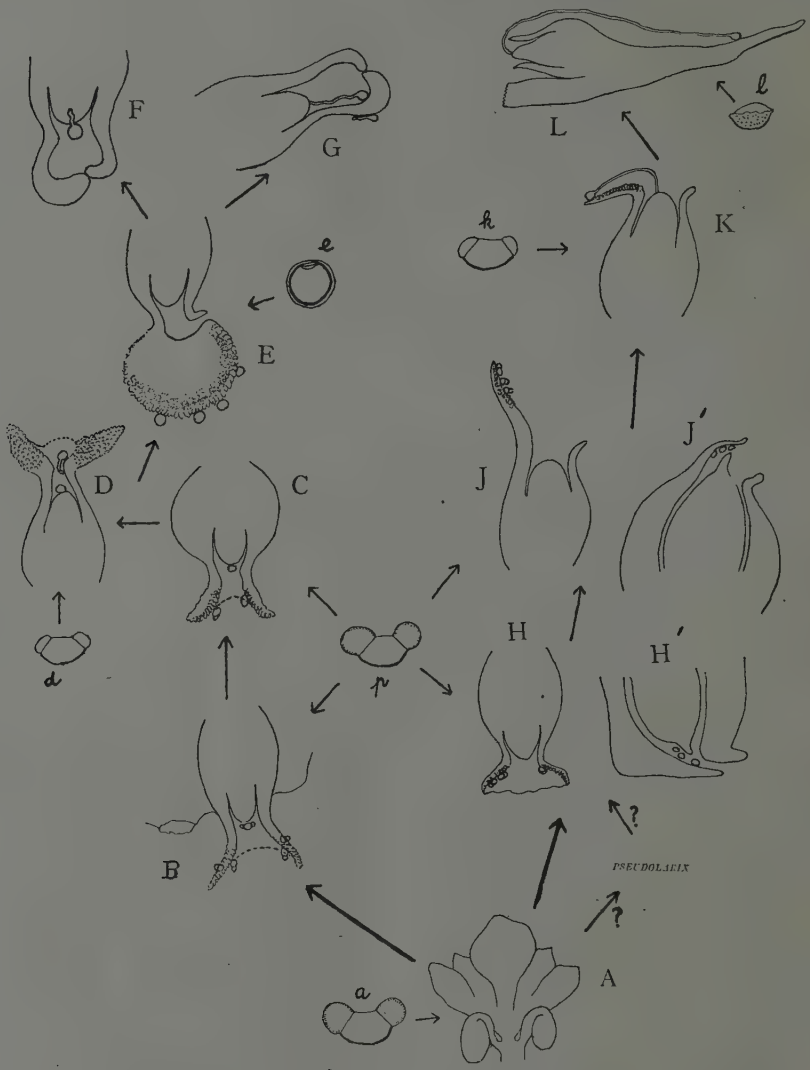

FIG. 2. Pollination behaviour in the two series in the Pinaceae. (Diagrammatic). A. *Pseudovoltzia Liebeana* and *a*, its pollen. B. *Pinus* type. C. Common *Picea* type. D. *Picea orientalis* and *d*, its pollen. E. Young *Larix—Pseudotsuga* type and *e*, its pollen. F. Later *Larix* type. G. Later *Pseudotsuga* type. H, H^1. Young and later stages of *Abies* type. J, J^1. Young and later stages of *Cedrus* type. K. *Tsuga Pattoniana* and *k*, its pollen. L. *Eutsuga* type and *l*, its pollen.

In centre, *p*, pollen common to *Pinus*, *Picea*, *Abies* and *Cedrus*. Dotted line across micropyle in B, C, D indicates fluid exudate. For explanation of *Pseudolarix* see text.

development from the micropylar edge of stigmatic expansions on which the pollen grains may be caught before the exudation of fluid begins. These are relatively thin in *Pinus*, 2 B, but commonly broader and more succulent in *Picea*, 2 C, which thus shows the tendency to an increasing stigmatic function of the micropyle which is so characteristic of this series.

Both also show an interesting physiological adaptation which may well have been a feature of the Permian types although naturally that can never be determined. The grains are easily wetted by the pollination fluid as it wells up through the micropyle, and so slip readily under its surface. Shortly after such immersion a rapid reabsorption of the fluid takes place. This can be complete in ten minutes or even less.

There are numerous minor variations in this mechanism. The original papers can be consulted for fuller details, but it is worth mentioning that in some cases the pollination exudate may be secreted from the ovules just before the pollen begins to fly. In such cases the pollen may be caught directly in the fluid, as must have occurred in the basal type, and the stigmatic function of the micropyle may thus play a minor role.

B. The Picea orientalis *type.* In all species of *Pinus* and in most of *Picea* the ovulate cones, as already noted, stand rigidly erect, but in *P. orientalis* the young cones hang downwards so that the ovules, though morphologically inverted, lie, in fact, with the micropyles directed upwards, Fig. 2 D. Further, the stigmatic function of the micropylar area is much more pronounced, the extensions forming two thick succulent flaps between which only a narrow slit leads into the ovular cavity, from which a normal fluid exudation takes place. But, in relation to the erect position of the ovules, the air-sacs on the grains are much reduced in size, Fig. 2 *d*, so that the grains quickly sink through the slit down to the nucellus. If, however, the grains are numerous some may get massed together and held at the micropylar slit, and some of these may send out a short pollen tube.

The special interest of these features in *P. orientalis*—the departure from the erect position of the cone, the increased stigmatic function, the reduction of the air-sacs, and the pollen germinating, although unsuccessfully, elsewhere than on the nucellus—is that they indicate the manner in which the *Larix—Pseudotsuga* type could have arisen.

C. The Larix—Pseudotsuga *type.* This type shows, then, an extreme advance on the *Picea orientalis* type. The stigmatic function of the micropylar area has here become dominant, a large swollen stigma, Fig. 2 E, developing, which covers the opening. There is no fluid secretion at the time of pollination, and it is clearly of interest in relation to this that the large pollen grains caught externally on the stigma have completely lost their air-sacs, Fig. 2 *e*, and with them the capacity to float. These grains have become so specialised from the primitive type that they show no real vestige of the germinal furrow, the wall being uniform over practically the entire surface. Dubois (1938) however figures a small circular area situated at the distal end and thinner than the rest of the wall. This may represent the last vestige of a furrow.

Inversion and invagination of the stigma brings the grains within the ovular cavity.

Pseudotsuga probably shows a slightly more advanced stage than *Larix*. The cones show no geotropic reaction at pollination but stand at any angle between an erect and horizontal position depending on the directional lie of the actual bud and the branch that bears it. The characteristic drooping position of the older cones is one which is only gradually assumed long after pollination. Further, the pollen remains attached to the inner invaginated surface of the stigma, and there germinates, the long tube growing down the micropylar canal to reach the nucellus, Fig. 2 G. Grains left outside, even those that happened to lodge near by, may send out a short tube. Thus the features associated with the flotation mechanism of the basal type—the erect position of the cones, the fluid secretion, the lateral air-sacs orientating the pollen with the germinal furrow in contact with the nucellus, and the subsequent germination of the grains thereon—have all been obliterated.

Larix, however, still retains the erect position of the cones at pollination, the ovules being thus always strictly inverted, Fig. 2 F. The grains, some time after the inversion of the stigma, become free and lodge on the nucellus, and here only, as in *Pinus* and *Picea*, can they germinate. It is not known how this transfer occurs, since the grains, without air-sacs and heavier than water, must *rise upwards* in the micropylar canal to reach the nucellus. There is, however, a possibility that a delayed fluid secretion within the now closed ovule may, on reabsorption, drag the grains up with it. *Larix* then still retains the basal feature of pollen germination on the nucellus, and possibly also some variant of an ovular secretion, so that *Pseudotsuga*, with the four major factors fully expressed, is, among living forms, the culminating type of this series.

The *Abies—Tsuga* series is indicated on the right side of Fig. 2. This series shows phenomena in some respects parallel to those of the *Pinus—Pseudotsuga* one, but the end result is different. The whole series in general is characterised by the complete suppression of any fluid exudate at pollination, and by a loss, instead of an intensifying, of the stigmatic function of the micropyle.

D. The Abies—Cedrus *type.* The mechanism in *Abies* appears to be nearest to the basal type. Indeed, when it first came under observation it was long thought that a fluid exudation should still take part in the pollination. The cones stand rigidly erect. The ovules, thus inverted in fact, Fig. 2 H, show a definite micropylar canal. The pollen grains, Fig. 2 *p*, have well developed air-sacs. Thus, although a fluid exudation at pollination is absent, the ovules impress the observer as differing only slightly in their physiological nature from the ancestral secreting type. The micropylar area, though still fairly symmetrical, has become splayed out as a shallow stigmatic funnel on which the grains are caught. The pollen, however, neither lodges on the nucellus nor sends tubes down to it, but the micropyle bends over and the nucellus grows up, Fig. 2 H, to make contact with the nearest grains. In some species, only the grains actually in contact with, or very close to, the upgrowing nucellus germinate ; in others, grains a little further out on the stigmatic surface may grow also.

Cedrus shows a somewhat specialized variant of the *Abies* type. The cones do not stand geotropically erect, although they often appear to do so. Actually they stand at right angles to the branch on which they are borne, and on drooping or oblique branches may lie at any angle to the vertical. Once more with the

disappearance of the flotation mechanism the geotropic sensitiveness of the cone is also suppressed. The micropyle area is also very unsymmetrical, expanding as a thin one-sided stigmatic flare, Fig. 2 J, which contracts to a slit on the opposite side. The pollen, Fig. 2 *p*, still carries air-sacs though relatively a little smaller than outlined. The subsequent development however resembles that in *Abies*, the stigmatic flare bending over, and the nucellus pushing up to make contact with the grains, Fig. 2 J^1.

This *Abies* type of behaviour departs so far, in its later phases, from the basal type as to suggest that there must have existed, or possibly still exists, some type intermediate between them. This type might well show a splayed-out stigmatic funnel but still associated with a flotation mechanism. It is just possible that this behaviour may be shown by *Pseudolarix*. Although sufficient cones were never available to permit continued personal observation of the mechanism here at work it is of interest that, although its young ovule closely resembles that of *Abies*, the pollen grains become lodged on the nucellus while it is still deep in the ovule, as if a flotation process were still at work. It is not formally included in Fig. 2.

E. The Tsuga Pattoniana *or* Hesperopeuce *type.* In the genus *Tsuga* a small group of species are included in the special section *Hesperopeuce*, of which the best known is *Tsuga Pattoniana*. In addition to the general character of the section this species differs from those in the other section, *Eutsuga*, in the possession of air-sacs on its pollen. The nature of the grains in other species in *Hesperopeuce* has not been described.

Behaviour here is that of a modified *Cedrus* type. There is, of course, no exudate, and the young cones, showing no geotropic reaction, lie roughly horizontal or droop a little. The micropylar edge expands again as a stigmatic flare, Fig. 2 K, in form intermediate between *Cedrus* and *Abies* but somewhat reflexed, and to it the pollen grains, Fig. 2 *k*, with rather small air-sacs, adhere. There is no bending forwards of the stigmatic flare, which becomes even more strongly reflexed, but at an early stage after pollination the nucellus grows up like a plug into the micropylar canal and protrudes slightly. Further, the possibility of pollen germination at some distance from the nucellus is here a working fact. Grains anywhere on the stigmatic area germinate readily *in situ* the tubes growing directly to penetrate the nucellus. Grains at some distance from the nucellus on the edge of the ovule or on the scale nearby also germinate, and produce quite long tubes which however grow erratically.

Tsuga Pattoniana seems to present a condition which principally differs from the *Cedrus* type only in the simple physiological feature that the pollen can germinate independently of the direct influence of the nucellus. In *Abies* and *Cedrus* a long delay ensues between pollination and growth of the pollen tube, which does not take place until the nucellus has pushed its tapering apex close to the grains. Although not lodged on the nucellus by any flotation mechanism the germination of the grains, in these two genera, is still physiologically related to some nucellar influence just as it must have been in *Lebachia*. In much the same way in the *Pinus—Pseudotsuga* series a nucellar influence remains dominant in *Pinus*, *Picea*, and *Larix*; only in the culminating type *Pseudotsuga* has the physiological change been established permitting independent pollen germination.

No satisfactory function can be readily associated with the air-sacs on the pollen in *Abies*, *Cedrus*, and *Tsuga Pattoniana*. They seem to be simply vestigal and harmless structures not yet dropped in development.

F. The Eutsuga *type.* This is an advanced development of the last type. It is characterised by the absence of air-sacs from the grains and of any stigmatic functioning of the micropylar area, which is simple and symmetrical, the pointed apex of the nucellus being flush with it. With no stigmatic surface or exudate present the bladderless grains may lodge anywhere on the cone scales, and over these the tubes grow in a surprisingly direct manner, like fungal hyphae, to penetrate the nucellar tip.

Although the grains are bladderless, thus paralleling the stage reached in the other series in *Larix* and *Pseudotsuga*, they are not as specialised as in these two genera. A description and outline drawing of the grain of *Tsuga canadensis* is given by Dubois (1938). The proximal surface is thicker walled and more coarsely ornamented than the distal, and equatorially round the grain runs a slight ridge, Fig. 2 *l*, which corresponds in position to the more pronounced ridge which encircles the grain in many species of *Abies* just above the upper edge of attachment of the air-sac. It is clear from the account given by Dubois (1938) and from comparison with some fossil *Tsuga* grains referred to by Wodehouse (1938) that the bladderless condition of the pollen in *Eutsuga* is derivative from the two-winged type; they are grains which, geologically speaking, have only recently lost their air-sacs.

It is unlikely, though always possible, that the highly perfected grain in *Larix* or *Pseudotsuga* arose at one step from the typical *Pinus* type. It is of interest then to find, even if in a different line, a grain type, as in *Eutsuga*, intermediate between the two extremes. Some fossil species of *Larix* or *Pseudotsuga*, or possibly even *Picea*, probably had grains of this type.

The behaviour in *Lebachia* is certainly markedly different from that in *Eutsuga*; but this latter type is clearly the result of a series of progressive changes from the former, many steps in the change being still to be seen fixed in other living related types. This *Eutsuga* type is important as it bears directly on conditions in the podocarps and the araucarians. In the latter particularly this behaviour is closely paralleled except that the grain has become almost as specialized as that in *Pseudotsuga*.

Thus from the basal *Ullmannia—Pseudovoltzia* type of pollination mechanism two general lines of development appear in the Pinaceae. In both can be seen the loss by the cones of their strong geotropic habit, the loss from the ovule of a fluid exudate, its replacement by a stigmatic functioning of the micropyle, the loss of the air-sacs from the grains, and pollen germination independent of nucellar influence; in other words, the primitive flotation mechanism is ultimately suppressed and replaced in both lines, but in a different manner in each. In one line, the *Pinus—Pseudotsuga* line, a stigmatic function of the micropyle, originally developed in association with a still functioning pollination exudate, ultimately became dominant with the loss of this latter; the pollen grain meanwhile becoming so specialized as to lose the primary characters of the ancestral flotation type. In the other line a stigmatic functioning of the micropyle early replaced completely the

suppressed pollination exudate but did not become dominant. Pollen germination, free from nucellar influence, here became the most striking feature, so that ultimately even the stigmatic function of the micropyle was lost, and bladderless grains lodged at random on the cone scales sent long tubes to reach the nucellus.

THE PODOCARPACEAE.

This family shows so much wider a range in vegetative structure and cone form than the Pinaceae that an even greater range of pollination mechanisms might be expected in it. This is probably not the case. Little attention, however, has been given to pollination phenomena in the family, the only published data being those on *Saxegothaea*, summarized and extended by Doyle and O'Leary (1935 a). Actually there is little doubt that the type there shown is exceptional and specialized, but some recent personal observations on *Podocarpus* have proved useful in considering the family as a whole.

Tentative conclusions are illustrated diagrammatically in Fig. 4. As the Podocarpaceae are characterized by having a single, primarily inverted, ovule in relation to a bract the suggested lines in the family are based on the *Ullmannia* type, Fig. 4 A.

A. The Podocarpus *type.* Observations have been made on *P. andinus*, one of the simplest living species, and on one of the more advanced forms, *P. nivalis*. As the mechanism in both is essentially the same, and as less complete observations on *P. salignus* and *P. latifolius* seem to agree closely, the pollination type must be reasonably uniform within the genus. The mechanism, while very similar to that of *Pinus*, is a little simpler, and seems indeed to be an actual retention of what that in *Ullmannia* must have been.

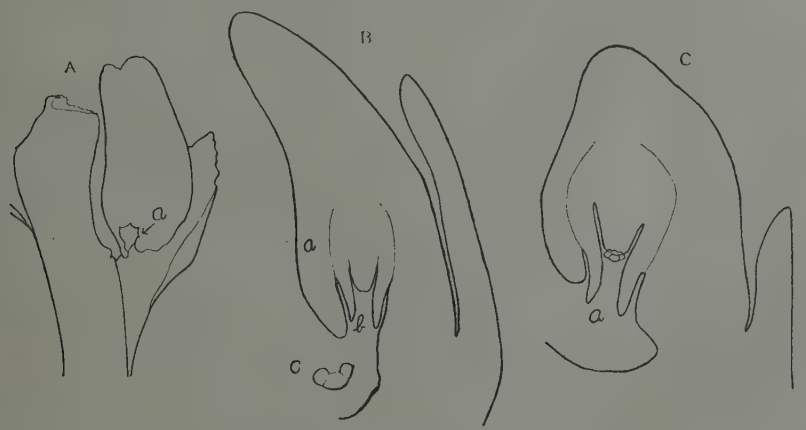

FIG. 3. Strobilus units in *Podocarpus*. A. *P. andinus*, solid view; *a*, arch-like opening under epimatium. B. Same in section; *a*, epimatial tissue; *b*, micropyle; *c*, pollen grain. C. *P. nivalis* similar stage in section; *a*, micropyle.

P. andinus, as is well known, has special ovulate branchlets which carry a number of widely spaced bracts. In the axil of each bract lies a stalked axillary structure which bears a single partly embedded and inverted ovule. One such reproductive unit is shown in the solid in Fig. 3 A and in section in Fig. 3 B. The condition is easily derived from the plan of structure of *Ullmannia*, Fig. 4 A. Early growth of the axillary scale, such that the ovule is recessed and covered, can readily produce the so-called epimatium tissue, Fig. 3 B*a*, which so completely obscures even the micropyle of the ovule proper in Fig. 3 A. The whole ovulate branchlet is delicately geotropic. In nature it stands erect irrespective of its place of origin on the vegetative stem, the zone of greatest response being just below its lowest ovule. If branchlets are removed and placed in water their lie is, of course, commonly altered but is rectified overnight. When actively growing at pollination time this can be repeated, producing almost an S bend in the lower part, which latter may be only half an inch long. The ovule thus lies with the micropyle pointing almost vertically downwards.

P. nivalis shows a typical *Eupodocarpus* branchlet carrying two, or only one, ovule. The branchlets are quite short in this species, but show an equally delicate geotropic response, which occurs most markedly at the junction of the short narrow stalk and the swollen podocarpean foot. Clearly here too the inverted ovules point vertically downwards.

The micropyle in both is symmetrical and simple showing no stigmatic tendency. This micropyle area is, of course, double. The embedded ovule is completely covered by the epimatium, the lower edge of which forms a simple arch-like channel, Fig. 3 A*a*, within which lies, in *P. andinus*, the tubular micropyle proper, Fig. 3 B*b*. In *P. nivalis*, Fig. 3 C, the micropyle *a* projects beyond the arch as a short reddish tube, but it is not known if such minor differences affect the behaviour in any way. A copious pollination exudate is secreted in both, and in this the pollen grains are caught. These have two well developed lateral bladders, Fig. 3 B*c*, and float upwards orientated as in *Pinus*. Shortly after immersion of the grains, the fluid, again as in *Pinus*, is rapidly reabsorbed. The secretion seems to be continuous, not rhythmical, as in some species of *Pinus*, so that if pollen is not received at a suitable stage the drop increases and may even, under laboratory conditions, run down the side of the branchlet. Retraction under these conditions is slower or erratic, but, owing to the evaporating power of the air in early June when pollination takes place, this effect is seldom seen in nature in the open.

Clearly then the mechanism in *Podocarpus* is of the basal flotation type, lacking even any early stigmatic tendency. There is every reason to accept the view, based on gynostrobilus structure and features of gametophytic and embryological development, that *P. andinus* is the simplest living podocarp. It would appear then that the simple flotation mechanism is basal in the Podocarpaceae also, and derived, with little change, from ancestral Permian forms of the *Ullmannia* type.

B. The Saxegothaea *type*. Here the behaviour is quite different but is comparable to that in the *Eutsuga* type. There is no fluid secretion and no special geotropic response in the cones. The pollen grains, almost spherical and without bladders, Fig. 4 *g*, fall on the cone bracts, and, if within a certain range of the ovule ,send out tubes, Fig. 4 G, to reach the nucellus, which projects as a marked

bulge well beyond the micropyle. It was at one time thought (Norèn, 1908) that this was a stigmatic projection for pollen reception, but it is now clear (Doyle and O'Leary 1935 a) that it is developed for the reception of the tips of the pollen tubes, which, having penetrated it, remain dormant for about nine months.

Although no intermediate between *Podocarpus* and *Saxegothaea* are to be found among living forms there can be little doubt, in view of the conditions in *Podocarpus* and *Pinus*, that this behaviour in *Saxegothaea* represents in the family of the Podocarpaceae a development similar to that shown by the *Eutsuga* species in the Pinaceae. There are, of course, obvious differences, which need no repetition here, but they are only differences in detail. The lack of any geotropic response in the cones, the loss of the pollination exudate, the loss of the bladders from the grains, the growth of the tubes on the cone scales, these are all repeated. It is of further interest in this connection that, although *Saxegothaea* has retained many primitive features, its cone organization is best interpreted as an advanced derivative from the simple *Podocarpus* type marked by fusion and reduction of parts. Specialization in pollination behaviour has thus accompanied specialization in the cone.

When fewer data were available many earlier workers (*i.e.* Thomson 1909, Stiles 1912), impressed by the apparently simple nature of the grain in *Saxegothaea*, were of the opinion that this bladderless type of pollen was primitive in the podocarps, the winged grains of other genera being thus a new development in the family. Sinnott (1913), however, among others, held, on general comparative grounds, that the air-sacs were ancestral features now lost in *Saxegothaea*, a view recently supported also by Wodehouse (1935). The comparisons here drawn between the two series of pollination types, *Pseudovoltzia—Pinus—Eutsuga* and *Ullmannia—Podocarpus—Saxegothaea*, definitely establish the air-sacs as ancestral and basal in the podocarps.

C. Other podocarpean genera. Unfortunately no details are available concerning pollination behaviour in any of the genera other than *Podocarpus* and *Saxegothaea*, but from what is known of the structure of ovules and pollen grains it appears probable that behaviour in this family is more constant than in the Pinaceae, and that some variant of the podocarpoid flotation mechanism is characteristic of all the genera except *Saxegothaea* and possibly *Phyllocladus*.

Thus, in many species of *Dacrydium* the ovules, when young, seem to be definitely inverted in relation to the vertical, although the actual lie of the ovule may change rapidly with age. Since, further, most species of *Dacrydium* have normal two-winged grains which lodge on the nucellus, and since the micropyle seems to be, commonly, symmetrical and non-stigmatic, it is probable that we are here dealing with a simple flotation mechanism as in *Podocarpus*. In Fig. 4, therefore, B and the grain *b* represent in general both *Podocarpus* and *Dacrydium* in relation to the ancestral type suggested by *Ullmannia*. It is more than probable, however, that when details are available this single grouping will be shown to include a number of derivative mechanisms. This is suggested in Fig. 4 by the arrows and queries leading from the top right of B.

The ovule of *Microcachrys*, Fig. 4 D, as shown in Lawson's (1923 a) figures, is at least obliquely inverted with a long extended micropylar tube directed vertically downwards. The pollen, 4 *d*, which lodges on the nucellus, has typically three

large bladders round the distal part of the grain. For these reasons, and also because *Microcachrys* almost certainly is a member of a line in the podocarps distinct from the *Podocarpus—Dacrydium* one, it is shown separately in Fig. 4, although in general the pollination behaviour must conform to the basal podocarpoid type.

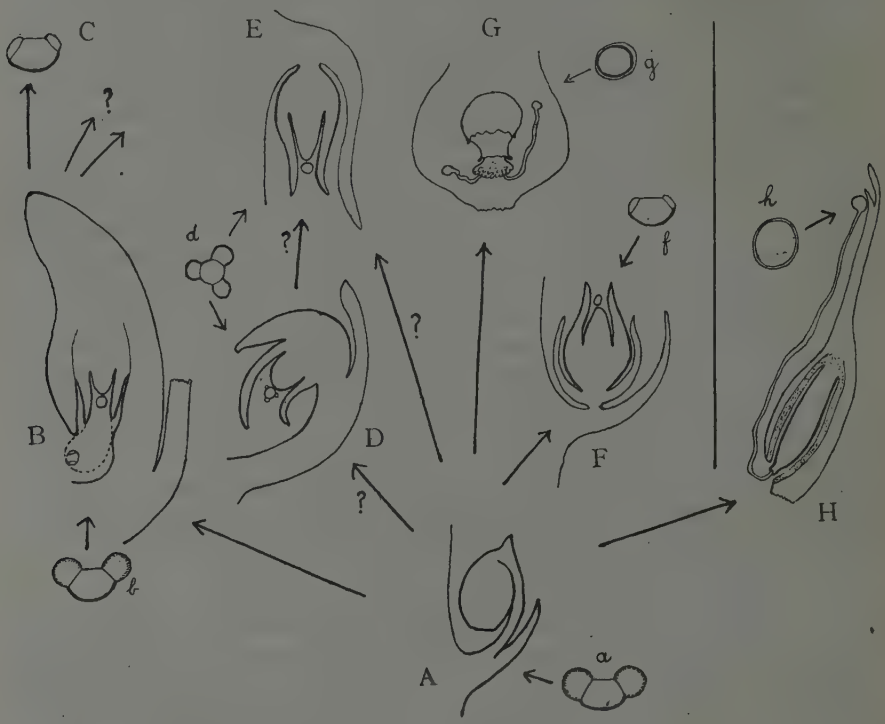

FIG. 4. Pollination behaviour in Podocarpaceae, B—G. and Araucariaceae, H. (Diagrammatic). A. *Ullmannia Bronni* and *a* its pollen. B. The *Podocarpus—Dacrydium* type and *b* its pollen; dotted line indicates pollination exudate. C. *Dacrydium* pollen type with rudimentary wings. D. *Microcachrys*. E. *Pherosphaera*. *d*. pollen of D and E. F. *Phyllocladus* and *f*, its pollen. G. *Saxegothaea*, and *g*, its pollen. H. Araucaria type and *h*, its pollen. Arrows and query to right of C indicate possible but undescribed *Dacrydium* derivatives. *Acmopyle* is omitted, as its behaviour is quite uncertain.

Pherosphaera, as a genus, may be a survivor of a distinct line or a derivative of the *Microcachrys* line as shown by the overlapping of their natural areas of distribution, the similarity in habit, the common possession of a three-bladdered grain, 4 *d*, and other features. This uncertainty is suggested by the query mark on the lines connecting A with D and E in the diagram, Fig. 4. But its pollination mechanism seems to be again essentially the simple podocarpoid flotation type. In *Pherosphaera* the axillary ovuliferous structure of the *Ullmannia—Podocarpus* plan has been reduced to a single morphologically erect ovule. But, according to Pilger (1926, Fig. 125), the young cone is inverted so that the actual ovules and

micropyles are again directed downwards, Fig. 4 E. The three-winged grains lodge on the micropyle (Lawson, 1923 b). Apparently the reduction in the cone structure has been accompanied by an inversion of the whole cone thus permitting the retention of the ancestral flotation mechanism.

The behaviour in *Acmopyle* is more problematic and is therefore omitted from Fig. 4. The grain has two well-developed air-sacs, but the form and lie of the young ovule of this rare plant are unknown. The name is derived from the form of the *maturing* ovule, in which the micropyle points upwards. At pollination however, the young ovule may well be strictly inverted, assuming the maturer position by later uneven growth, as so commonly occurs in *Dacrydium*. If so, a typical podocarpoid flotation mechanism would probably be operative in this case. The only figure available, however, of pollen in relation to the nucellus, a simple line drawing (Sahni 1920), shows an upgrowth of the apex of the nucellus into the micropyle with the grain proper separated from its surface by a length of the pollen tube; a condition which might indicate a behaviour along the lines shown by *Abies* in the Pinaceae.

Apart from the at present uncertain relationships of the genera mentioned they all seem to have retained the ancestral type of pollination mechanism or some simple variation of it with the doubtful exception of *Acmoyple*. Other forms, however, as well as *Saxegothaea*, seem to have departed more from the type. Thus in *Dacrydium*, as in *Tsuga*, an intrageneric modification in the pollen grains has taken place, as two species, at least, are reported as showing only rudimentary air-sacs—*D. Gibbsieae* (Wodehouse 1935) and *D. cupressinum* (Sinnott 1913). In what way the pollination mechanism is affected, if at all, is unknown. The fact is indicated in Fig. 4 C and the nearby query marks. Further, in *Phyllocladus* the ovule seems to stand at least obliquely vertical and thus with the micropyle above, Fig. 4 F. The pollen grains, with only rudimentary wings, Fig. 4 *f*, undoubtedly lodge on the nucellus, and, as in *Picea orientalis*, may do so by sinking in the pollination fluid, which is subsequently reabsorbed; but again the actual behaviour is unknown. However, even these modifications in *Dacrydium* and *Phyllocladus*, in view of the known cases in the Pinaceae, must also be considered direct derivatives from the ancestral flotation type.

The marked difference in the gynostrobilus in living podocarps, coupled with many features in gametophytic and embryological development, suggest, as indicated in Fig. 4, an early divergence of several lines from the primitive podocarpoid stock. Along several of these lines the basal Palaeozoic type of pollination mechanism seems to have been retained. It can be seen, at least in principle, in the lines represented to-day by *Podocarpus*, the related *Dacrydium*, *Microcachrys*, *Pherosphaera*, and possibly in *Acmopyle*. Within *Dacrydium* modifications of an unknown type have probably occurred. As the three-bladdered condition in *Microcachrys* and *Pherosphaera* does not directly affect the *pollination mechanism*, the grain floating and orientating itself as in the normal, it need not here be further discussed, although it may obviously bear on general questions of intergeneric relationships. It does suggest however that the primitive pollen grain in the podocarps may have possessed a bladder all round the distal half, a bladder which evolved into two air-sacs

in some lines and into three (or more) in others. As in the Pinaceae the grain figured in Fig. 4 *a* may be taken as one with two lateral air-sacs or one with a continuous circular bladder seen in section.

The only major modifications known to have become established in the family are those shown in *Phyllocladus* and *Saxegothaea*. The exact nature of the former is obscure, but it is clear from the preceding discussion that the behaviour in *Saxegothaea* is exceptional. It is an advanced specialized type but quite comparable to that developed in the Pinaceae in *Eutsuga*.

Only in *Podocarpus* and *Saxegothaea* have the actual facts been observed and recorded. Proper conclusions for the family as a whole can only be come to when the data for the other genera and divergent types have similarly been put on record. And this can only be done by observations, *in situ* in the field, of the actual processes during the pollination period, which is usually of short duration, often not more than a week.

The Araucariaceae.

The pollination mechanism in the araucarians, *Araucaria* and *Agathis*, first described by Thomson (1907), is now well known. It is essentially similar to the *Eutsuga* type. The pollen grains, Fig. 4 *h*, which are without air-sacs, lodge on the cone scales, and the tubes grow towards the ovule, the apex of the nucellus projecting to receive them, Fig. 4 H. The grains, however, are more advanced than in the hemlocks, and tube growth is more vigorous.

When first described this phenomenon roused much interest, and many earlier workers, impressed by the archaic characters supposed to be shown by the family, discussed the possibility of this type of pollination being basal in the conifers as a whole. This idea has been, perhaps, best elaborated by Burlingame (1915). If, he argued, the gymnospermous ancestors of the conifers all had a pollen chamber for reception of grains caught by a pollination drop exuded from the micropyle, as is still shown by living Cycads and *Ginkgo*, it is difficult to see how pollen reception on the cone scales and its germination there could have arisen. He suggested that such would have been a highly disadvantageous change. For the Pteridospermae, with exposed ovules on open fronds, direct ovule reception of the pollen would appear to have been the only possible type, but for the ancestral conifers he postulated that, in these, cone formation, the protection of ovules by spreading scales, was developing at the same time as the seed was being evolved. In spite of the fact that the ovules of all the then known fossil gymnosperms possessed a pollen chamber mechanism, he further postulated the existence of other, presumably earlier, types, in which this feature was lacking. In these, he suggested that pollen reception could well have been on the scales of the cones then in process of organization. In subsequent modification only grains closer, and then still closer, to the ovule could achieve successful tube growth ; and so direct ovular reception was finally effected. Such ovular reception became characteristic of all the early conifer families except the araucarians, which, he claimed, still retained the archaic type of cone reception—the so-called protosiphonogamous mechanism.

In the light of present knowledge it is hardly necessary to criticise this view except in very general terms. Undoubtedly, we do not know how fertilization

was effected in the pregymnosperm phyla when the gynosporangium was becoming the ovule, but that at the moment is immaterial, as it refers to an earlier problem which does not here arise. It seems quite definite, however, when Florin's work is added to previous data, that the immediate conifer ancestors, in Carboniferous and Permian time, all had direct ovular reception of the pollen, so that the araucarian type must have derived from this. Knowing, as we do, so little of the physiology and biology of these pollination processes how can any one modification be dismissed as a highly disadvantageous change? It cannot be denied, for example, that scale reception and germination in *Eutsuga* have been derived from a type with direct ovular reception, and the hemlocks are a successful and widespread group. The real problem would appear to be concerned, not with modifications in the physiological behaviour of pollen tubes, but rather with the origin of any pollen tube at all. The fossil record is still too obscure for discussion of that problem, but it is tempting to suggest that the development of the two-winged condition in the ancestral grain, orientating a relatively thin germinal area into contact with nucellar tissue, may have been related to the change in that area from a fission zone to a zone which underwent extension growth as in a root hair.

The araucarians, like the podocarps, show a single inverted ovule, and the pollination mechanism of the ancestral type must have closely resembled that of *Ullmannia*. In Fig. 4, therefore, the araucarian type, H, is shown as related to the same basal *Ullmannia* type, A, as the Podocarpaceae. Indeed *Ullmannia* itself, in habit and in cone, points directly to the araucarian form, which can readily be derived from it by reduction of the axillary ovuliferous scale and its fusion with the subtending bract. Further, Wodehouse (1935) describes, on the grain of some species of *Araucaria*, traces of a vestigal germinal furrow indicative of a grain in which air-sacs have but recently been suppressed. The grains of the more advanced genus, *Agathis*, do not show even this vestigal trace; they are on the same level of advance as *Pseudotsuga*. The bladderless condition here is thus comparable with that obviously developed by a similar loss of bladders in *Larix*, *Pseudotsuga*, *Tsuga*, and *Saxegothaea*.

Although, then, the araucarians may have retained many features of an archaic type it is suggested that they show a pollination behaviour of an extremely advanced character. The mechanism, derived ancestrally from the same basal flotation type as that in the Pinaceae and the Podocarpaceae, has developed in a manner comparable to that shown by *Eutsuga*. Advance has gone even farther in the araucarians as the grain is more specialized and the pollen tubes show greater power of growth. The changes in the Pinaceae leading to the *Eutsuga* type may have been quite recent, but in the Araucariaceae the evolution must have taken place much earlier, the intermediate species or genera being now extinct. Such intermediate araucarian types, comparable perhaps to *Cedrus*, *Abies*, or *Tsuga Pattoniana*, are probably waiting discovery in the early Mesozoic strata.

THE OTHER FAMILIES.

The Taxodiaceae, Cupressaceae, and Taxaceae (including *Cephalotaxus*), all show the simple pollination-drop mechanism with wingless grains, a type shared

also by the other living gynosperms. In these the micropyle is symmetrical and non-stigmatic, and the pollination fluid exudes through it as a round glistening drop in which the grains are caught, the grains lacking not only air-sacs but, in most cases, even any vestige of a germinal furrow or pore.

Relatively little critical examination has been made of this mechanism. Tison (1911) gives some interesting data, but his observations are still rather general. More precise examination over a wider field is needed to elucidate the nature of the variations which undoubtedly occur. Apparently all these wingless grains sink in water or in fluid of the concentration of the drop. It might be expected then that the ovules would stand universally erect and so permit the grains to roll down the micropylar canal to the nucellus. But in many—*Taxus*, *Cryptomeria*, species of *Cupressus*, and others—although the young ovules are morphologically erect the cones are strongly inverted, so that, in fact, the micropyle and drop are turned downwards. The grains when received first fall away from the micropyle opening. In others the young ovules may be, in fact, horizontal, oblique, or erect. How the grains reach the nucellus, especially of the inverted ovules, is not clear, although there is some evidence, also noted by Tison (1911), that rapid retraction of the fluid may occur after a certain period. Again, in most, probably in all, of the grains concerned the intine is thick and can swell enormously in water throwing off the extine. In which species this occurs *in* the drop before retraction and in which only when the grains have reached the nucellus has still to be determined. The swelling may be rapid or slow; but some grains which swell slowly in water will, after a brief immersion in the pollination fluid followed by transfer to water, show an almost instantaneous swelling. Such points are merely touched on here to indicate the nature of the problems which arise and which need solution in relation to the detailed working of the variants in the mechanism. But in all cases the pollen grain becomes lodged on the nucellus, and there germinates.

Apart from the details of such problems, whose solution merely depends on suitable simple experiments and close observation of living material at the pollination period, a relation of the mechanism in general to the Permo-Carboniferous types may be suggested. The ovules themselves have changed little from the *Lebachia—Ernestiodendron* type, except of course in the feature common to all living conifers, the absence of a pollen chamber. The micropyle is fairly symmetrical, and lacks, as far as is known or recorded, any stigmatic device, but readily permits the retention and display of the characteristic drop. The principal change from the ancestral type, then, is in the grain characterized by the complete suppression of any flotation bladder, the absence of any vestige of a germinal furrow, and the thick swelling intine. Now there is no evidence that this grain ever passed through a clean-cut two-winged stage or one of its variants. That grain type seems primarily related to an inverted ovule associated with a cone axis which is sensitively geotropic and which maintains the inverted ovule more or less accurately in a vertical position. The families showing the simple pollination-drop type do not show typically a strictly inverted ovule at pollination. They may thus be related to some Permo-Carboniferous types in which the ovules remained erect. The grain then would be simply that of *Lebachia* with the balloon sac completely suppressed. The grain of *Lebachia* can hardly be said to possess a true germinal

" furrow," the distal germinal pole, not covered by the sac, being a small and more or less circular area. Any vestige of this area has completely disappeared in most of the grains of these living types, but it may well be that the small circular papillate area shown in the pollen of *Sequoia* and *Cryptomeria* represents the distal pole of the *Lebachia* grain.

These suggestions can, at present, be merely tentative. The taxads and the taxodinean conifers belong to two very divergent lines whose Permian ancestors may have been different. The evolution of pollination mechanisms, and ovular position in relation thereto, may have then followed quite a different path in the two groups. Thus, in *Phyllocladus* in the Podocarpaceae, complete suppression of the two rudimentary air-sacs could give a wingless grain associated with a symmetrical micropyle and a typical pollination drop, although, ancestrally, *Phyllocladus* must have been derived from a form with inverted ovules, two-winged grains, and a flotation mechanism like *Podocarpus*. In some of the living groups, now showing the simple pollination-drop mechanism, development may have taken place along some such lines. But, as living intermediates, such as illustrate progress in the *Pinaceae* and the *Podocarpaceae*, have not been observed in the families here concerned, and as their early fossil history has still to be determined with reasonable certainty, decision on the points here raised must await the uncovering of further fossil evidence. The possibilities have therefore not been illustrated by any diagram.

SUMMARY.

This paper deals with the relations of pollination mechanisms only, not with the relations of individual genera. Basal to the conifers as a whole is the type shown by Upper Carboniferous and Lower Permian forms such as species of *Lebachia* and *Ernestiodendron*. An erect ovule receives, in a fluid exudate from a simple micropyle, a pollen grain entirely covered by a large air-sac except for a small distal area. In the Upper Permian, as shown by species of *Ullmannia* and *Walchia*, there developed inverted ovules associated with grains of a modern type, *i.e.* with two distal air-sacs derived by suppression of the proximal part of the balloon sac. This type is basal in the Pinaceae, Podocarpaceae, and Araucariaceae. The air-sacs are flotation devices which float the grains up through the pollination fluid in the micropylar canal of an inverted ovule, and tend to orient them with the germinal furrow in contact with the nucellus.

From this two lines appear in the Pinaceae both ultimately showing loss of exudate, stigmatic development of the micropylar area, suppression of air-sacs from the grains, and pollen germination elsewhere than on the nucellus. The end result differs in the two lines. In the first—*Pinus*, *Picea*, *Larix*, *Pseudotsuga*—the ovular exudate is ultimately replaced by an increasing dominance of the stigmatic tendency culminating in *Pseudotsuga*, where however germination of the now wingless grains is still intraovular but not on the nucellus. In the second—*Pseudolarix* (?), *Abies*, *Cedrus*, *Tsuga*—the exudate is early suppressed, and the stigmatic function of the micropyle, never very marked, is ultimately replaced in *Tsuga* by pollen reception on the cone scales, over which long tubes grow from the wingless grains. *Tsuga Pattoniana*, with winged grains, is an interesting intermediate type.

In the Podocarpaceae *Podocarpus* shows a typical Upper Permian type with simple micropyle and no stigmatic tendency. In *Saxegothaea* scale reception and the germination thereon of wingless pollen has been achieved as in *Tsuga*. Most of the other divergent lines in the podocarps seem to have retained the basal *Podocarpus* type, or some variant of it, except *Phyllocladus* and some species of *Dacrydium*, which have only rudimentary air-sacs on the grains. Details of the pollination behaviour in these have not been observed.

The Araucariaceae, though derived from forms showing the Upper Permian flotation mechanism, show scale reception and germination thereon of wingless grains, *i.e.* development has paralleled that in *Tsuga* in the Pinaceae but is somewhat more advanced. Intermediate types are extinct.

The other families, Taxaceae (including *Cephalotaxus*), Cupressaceae and Taxodiaceae, show the simple pollination-drop type with wingless grains. Few details are available as to the actual functioning in this type or concerning the variants of it which may occur. The early fossil lines for these families are not clear. But tentative relations with the *Lebachia* pollination type are suggested.

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